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THE SEA LAMPREY

by VERNON C. APPLEGATE AND JAMES W. MOFFETT

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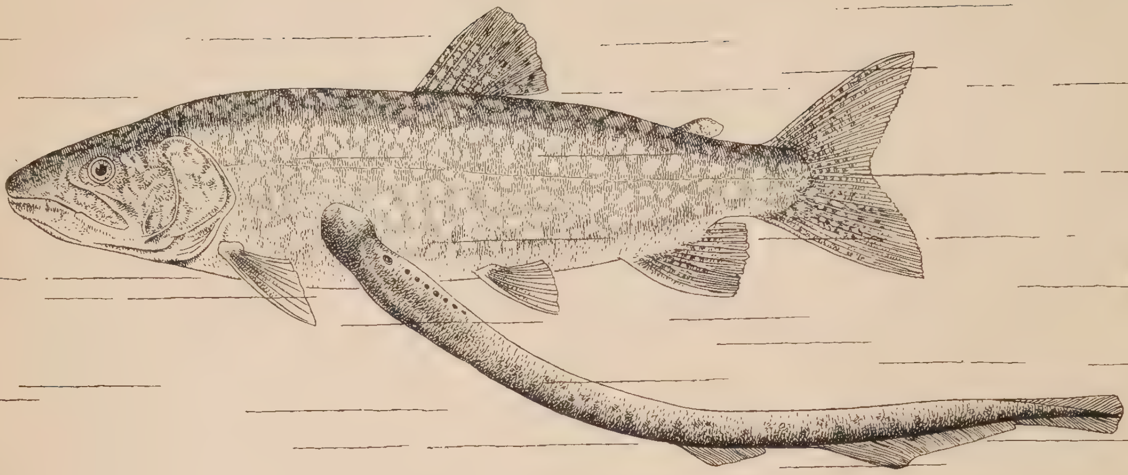
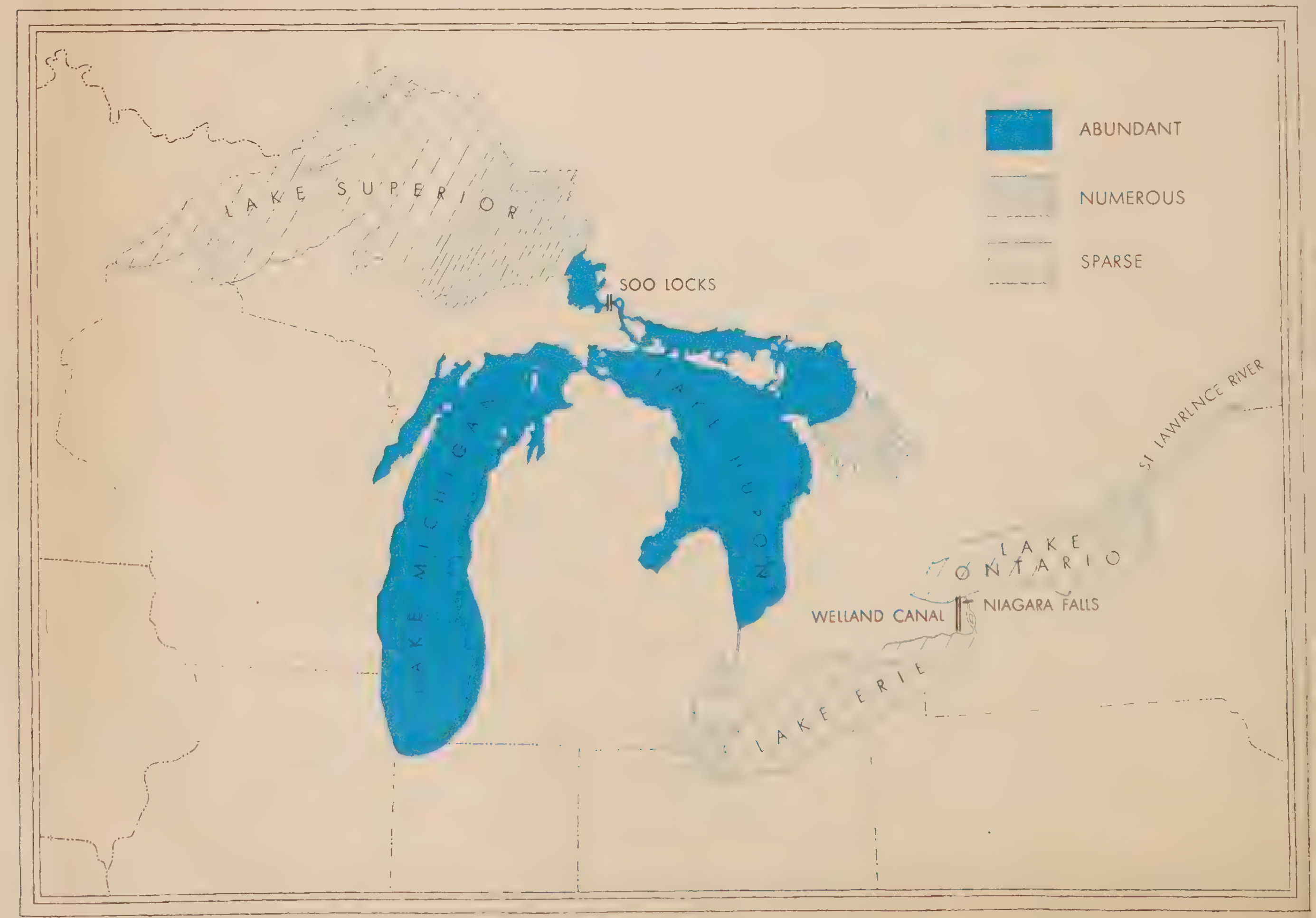


SEA LAMPREY FEEDS on a lake trout. The lamprey may remain attached to a fish for weeks. Some fish, however, die in as little as four hours. The adult lamprey ranges from 12 to 24 inches in length. Its back is dark blue and its belly silvery white.


ABUNDANT
NUMEROUS
SPARSE
LAKE SUPERIOR
SOO LOCKS
LAKE MICHIGAN
LAKE HURON
ST LAWRENCE RIVER
LAKE ONTARIO
WELLAND CANAL
NIAGARA FALLS
LAKE ERIE

SEA LAMPREY INVADED Lake Erie in the 1920s by way of the Welland Canal. In this lake, however, the lamprey did not flourish. By the 1930s the lamprey had reached Lake Huron and Lake Michigan. It is now becoming established in Lake Superior.

The Sea Lamprey

This eel-like creature fastens itself to fish and sucks their blood. Within the past 25 years it has invaded Lake Huron and Lake Michigan and destroyed their teeming population of trout

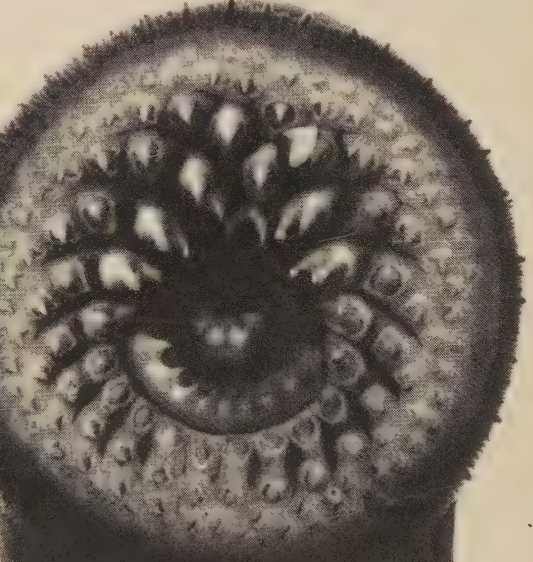
by Vernon C. Applegate and James W. Moffett

For more than 80 years fishing in the Great Lakes has been a sizable industry and a popular recreation for fishermen of the U. S. and Canada. Each year it yields a commercial catch of more than 100 million pounds of choice food, to say nothing of the millions of pounds caught by sportsmen. The most prized fish, and the backbone of the fishing industry, has been the lake trout. In good years the trout catch amounted to more than 15 million pounds, worth nearly $8 million. But in the past 15 years the Great Lakes trout has suffered a disaster. The U. S., preoccupied with more spectacular troubles on a global scale, has not paid a great deal of attention to this calamity in its own backyard, though it threatens to destroy an important industry and relaxation.

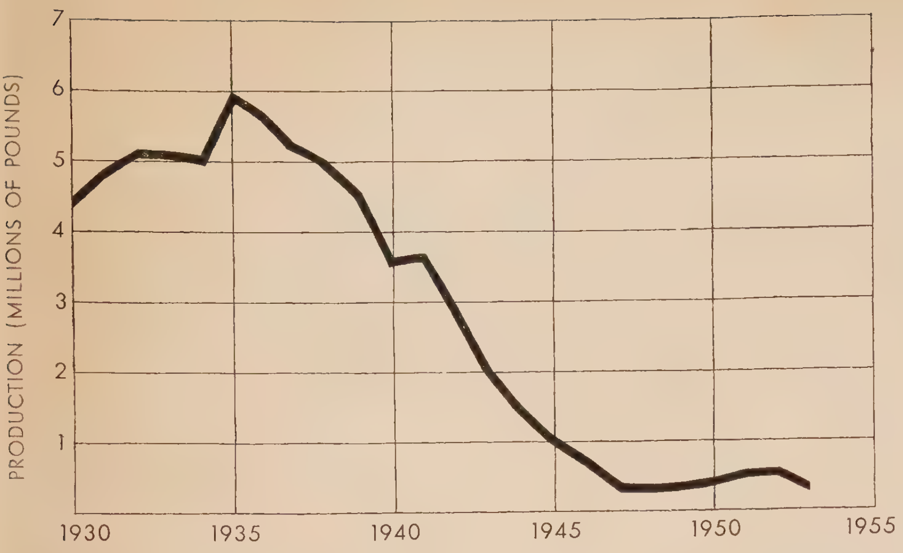
The trout catastrophe began in Lake Huron in 1939. The fish suddenly began to decline in numbers, and within 14 years it had all but disappeared from that lake; the catch dropped from more than five million pounds a year to 344,000 pounds in 1953. The same fate began to overtake Lake Michigan's trout in 1946, and the catch there fell from more than five and a half million pounds to a mere 402 pounds in 1953. Now the slaughter has started in Lake Superior and has begun to cut sharply into its annual trout catch of four and a half million pounds.

Neither overfishing nor weather nor disease is responsible for the annihilation of the trout. The culprit is an eel-like fish known as the sea lamprey. It is a murderous animal efficiently equipped with tools for destroying fish much larger than itself. The lamprey has a sucker-like mouth, sharp teeth and a tongue as rough as a file. Attaching itself to its victim with its mouth, it rasps a hole in the fish's body and sucks the blood and body juices; it is assisted in this by a substance in its saliva, called lamphredin, which prevents coagulation of the blood and dissolves the torn flesh. The victim thrashes about violently but cannot shake off its parasite. The lamprey, a swift swimmer with excellent vision, makes easy prey of fishes, because they are not alarmed by it and tend to ignore it until it strikes. Once it has gained a hold, the lamprey hangs on until it is satiated or the victim dies. A full-grown lamprey may kill a delicate fish such as the trout in as little as four hours. When the victim is more hardy, or the lamprey small, the parasite may cling and feed on the fish for days or even weeks. In the laboratory large lampreys stick to their victims for an average of about 40 hours if the fish survive that long.

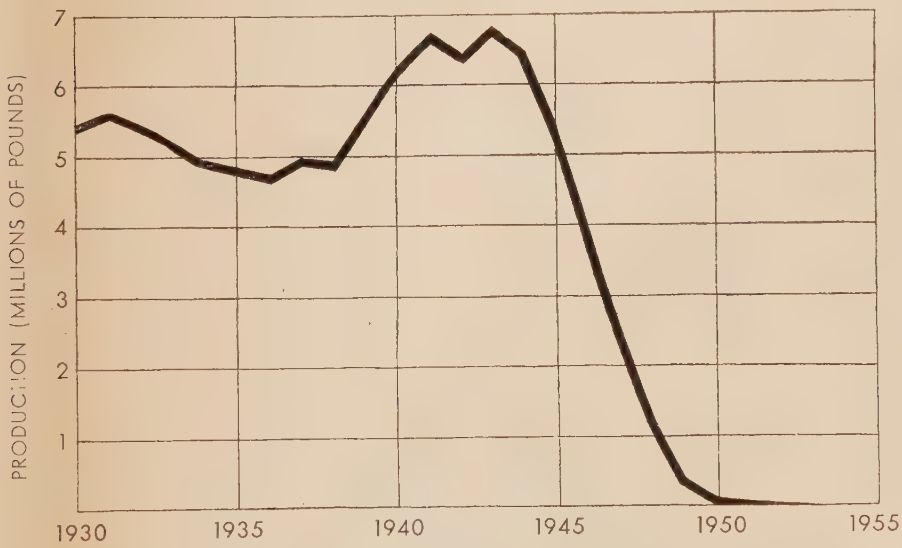
The sea lamprey is a newcomer to the upper Great Lakes. It is a marine species which, like certain salmon, hatches in a fresh-water stream, migrates to the ocean to spend its adult life, and then comes back to fresh water to spawn. In some places it has adjusted



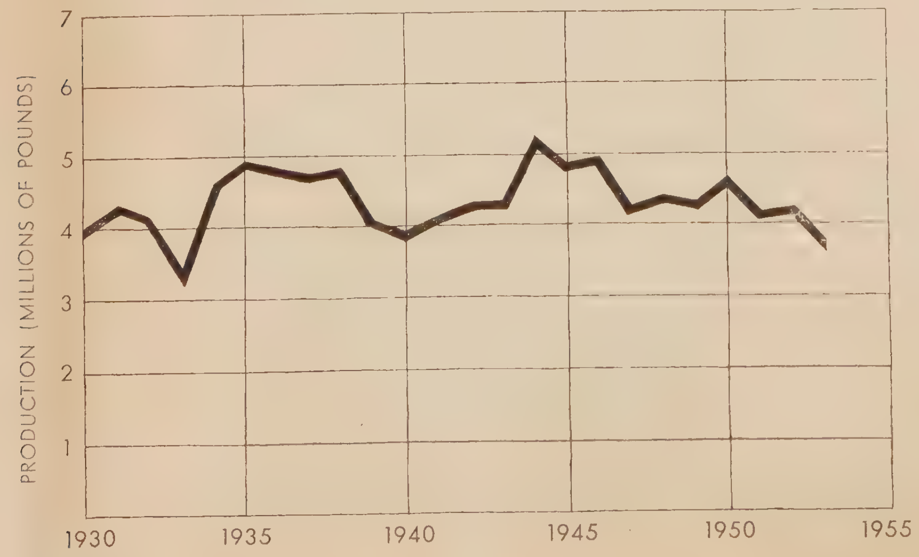
MOUTH of the sea lamprey is photographed through a flat piece of glass to which it is attached. The mouth is lined with horny teeth. In the center of the mouth is the rasped tongue.



LAKE HURON produced 5,998,000 pounds of lake trout in 1935 and 344,000 in 1953. At 1950 dockside prices the 1935 catch was worth $2,999,000; the 1953 catch, $172,000.



LAKE MICHIGAN produced 6,860,000 pounds of lake trout in 1943 and 3,000 pounds in 1952. At 1950 dockside prices the 1943 catch was worth $3,430,000; the 1952 catch, $1,500.



LAKE SUPERIOR does not yet show a catastrophic decline in trout production. However, production fell off from a high of 5,293,000 pounds in 1944 to 3,784,000 pounds in 1953.

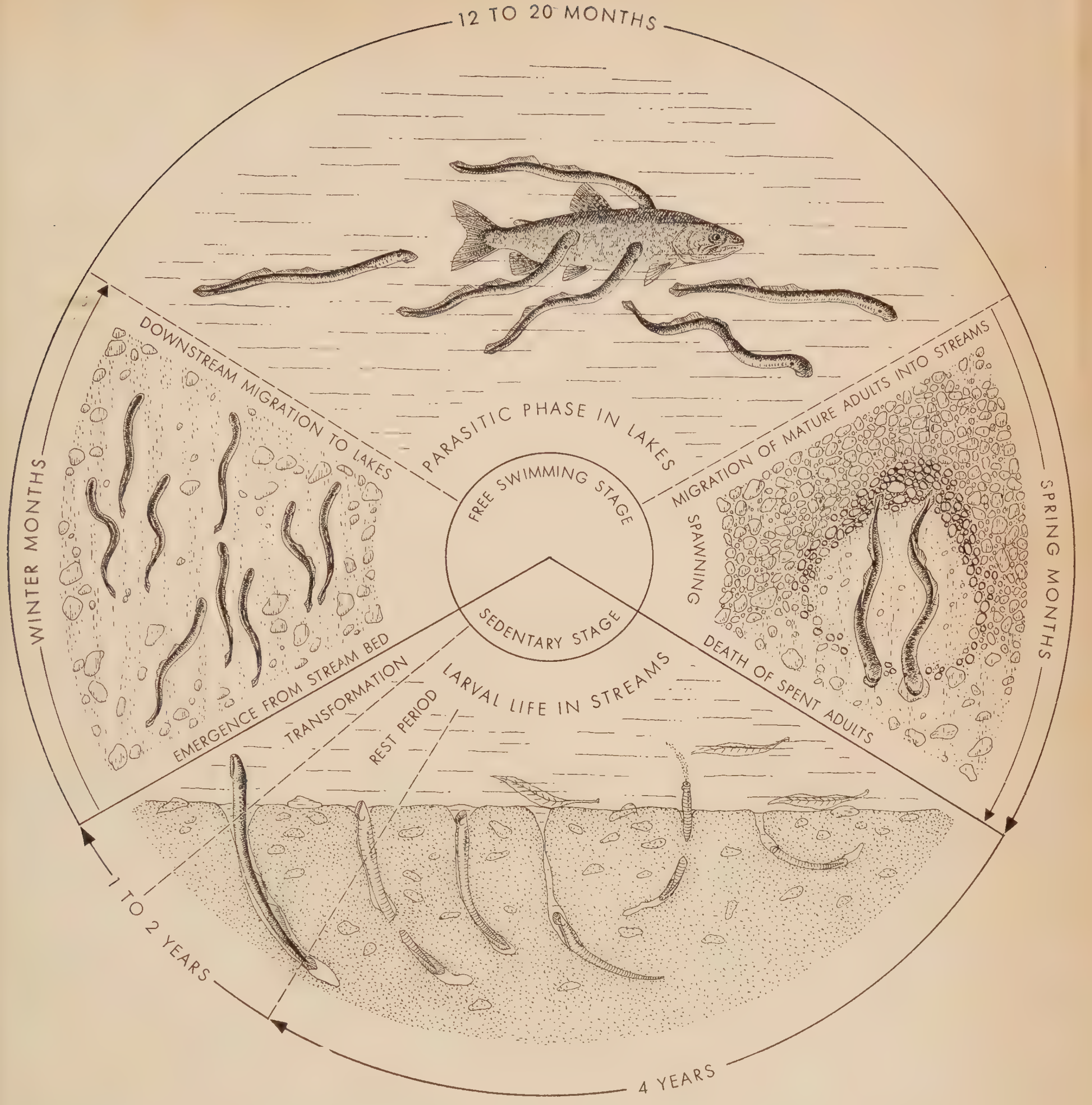
itself to spend its entire life cycle in fresh water, passing its adulthood in lakes instead of in the ocean. It is an old inhabitant, for example, of the St. Lawrence River and Lake Ontario. Until 1829 the Niagara Falls blocked it from migrating into the other Great Lakes. Then the building of the Welland Ship Canal provided a passage around the Falls to Lake Erie, but the lamprey seems to have been slow to take advantage of the route. No lamprey was seen in Lake Erie until 1921.

In Lake Erie the lamprey did not flourish; the waters were too warm and the spawning conditions poor. But by the late 1930s the destroyer had penetrated into the next of the Great Lakes, Lake Huron. Fishermen's nets began to bring up trout and other fish with ugly wounds on their bodies. Sometimes the fish had lampreys still clinging to them. Lake Huron was a particularly favorable environment for the lampreys; they multiplied rapidly and made great inroads into the fish of that lake. Meanwhile they also spread through the Straits of Mackinac into Lake Michigan and increased meteorically there. Apparently further migration into Lake Superior was slowed by the locks and dams at the head of Saint Marys River, but the lampreys finally cleared that hurdle and are now well established in Superior.

The kill of trout by the lampreys was prodigious. Experiments in laboratory aquaria have shown that during its period of active feeding a lamprey kills a minimum of 20 pounds of fish. As many as 25,000 spawning lampreys have been trapped in a single northern Lake Huron stream in a year; simple arithmetic shows that this one group must have destroyed 500,000 pounds of fish.

Commercial fishing for trout in Lakes Huron and Michigan came to an end several years ago. As the trout gave out, the lampreys turned more and more to other fish—whitefish, suckers, walleyes and so forth. Today much of the fishing industry in the Great Lakes is in serious economic difficulty. If the Lake Superior trout go, the industry there probably will collapse. To try to save the trout and other fish, the U. S. Fish and Wildlife Service, the Great Lakes states and Canada have been carrying on research and testing measures against the lampreys. A treaty for joint action by the U. S. and Canada was signed on September 10, 1954, and awaits ratification.

As in any pest-control problem, we must find the vulnerable points in the life cycle of the animal to attack it effectively. The life cycle of the sea lam-


12 TO 20 MONTHS
PARASITIC PHASE IN LAKES
FREE SWIMMING STAGE
MIGRATION OF MATURE ADULTS INTO STREAMS
SPAWNING
SPRING MONTHS
DEATH OF SPENT ADULTS
SEDENTARY STAGE
LARVAL LIFE IN STREAMS
REST PERIOD
TRANSFORMATION
EMERGENCE FROM STREAM BED
DOWNSTREAM MIGRATION TO LAKES
WINTER MONTHS
1 TO 2 YEARS
4 YEARS

LIFE CYCLE of the lamprey is depicted in this chart. The lamprey lives 6½ to 7½ years. The size of the segments in the chart do not correspond to the length of time the lamprey spends in each stage. The lamprey spends most of its life as a larva.

prey begins in the shallow riffles of a stream. Here it passes the major portion of its life as a blind, harmless larva. Of its approximately seven-year life span, a lamprey spends only the last 18 months in the lakes as a parasite. At the end of that time it goes back to the stream to spawn and die. Let us follow the cycle in some detail from the spawning stage.

The old sea lampreys begin their migration up the tributaries of the Great Lakes to spawn in early spring, the time of migration in each lake depending on the water temperature. They congregate in bays and in the estuaries of rivers during late winter, and when the stream temperature rises above 40 degrees Fahrenheit they start moving upstream. They seek out streams with a gravel or sand bottom and a moderately strong current.

Normally the male starts building the nest; then he is joined by a female who helps in the construction. They clear a small area, picking up stones with their sucker-like mouths and piling them in a crescent-shaped mound on the downstream side of the nest. When the nest is finished and the temperature of the stream is warm enough (over 50 degrees F.), the spawning begins. The female extrudes a small number of eggs; the male at once fertilizes them, and the eggs are carried by the current to the gravel rim of the nest, where they lodge in the spaces among the stones. Then the female lays another batch of eggs and the process is repeated. The eggs accumulating in the nest rim are covered with sand and additional stones. The pair go on producing fertile eggs until they are spent—after anywhere from one to three days. Then both partners die within a matter of hours.

The female has deposited from 24,000

to 107,000 eggs; the average is about 61,500. Fortunately less than 1 per cent of these eggs will hatch out into larvae.

Hatching takes 10 to 12 days. The hatched larvae remain buried in the sand and gravel until about the 20th day. Then the tiny creatures, only about a quarter of an inch long and hardly thicker than a fine needle, emerge from the nest and drift downstream until they reach quiet waters. Here they dive for the bottom and each digs an individual burrow. This will be its home for about five years, unless erosion washes it away. Throughout its larval life the young lamprey is blind and harmless. It sucks food, mainly microscopic organisms, from the water passing the mouth of its burrow. A filtering apparatus in its throat keeps out debris and passes food organisms to its digestive tract.

After four years the larva undergoes a striking metamorphosis. It develops large, prominent eyes, a round mouth lined with horny teeth, a filelike tongue and enlarged fins. Its slim body becomes dark blue above and silvery white beneath. The new young lamprey, some four to seven inches long, may emerge from its mud flat when late fall rains raise the river level, but usually it waits until the spring breakup and flood. It drifts downstream to the big lake and begins its parasitic existence, living on the blood of fish. Feeding upon a succession of hosts, it grows very rapidly, attaining a final length of 12 to 24 inches.

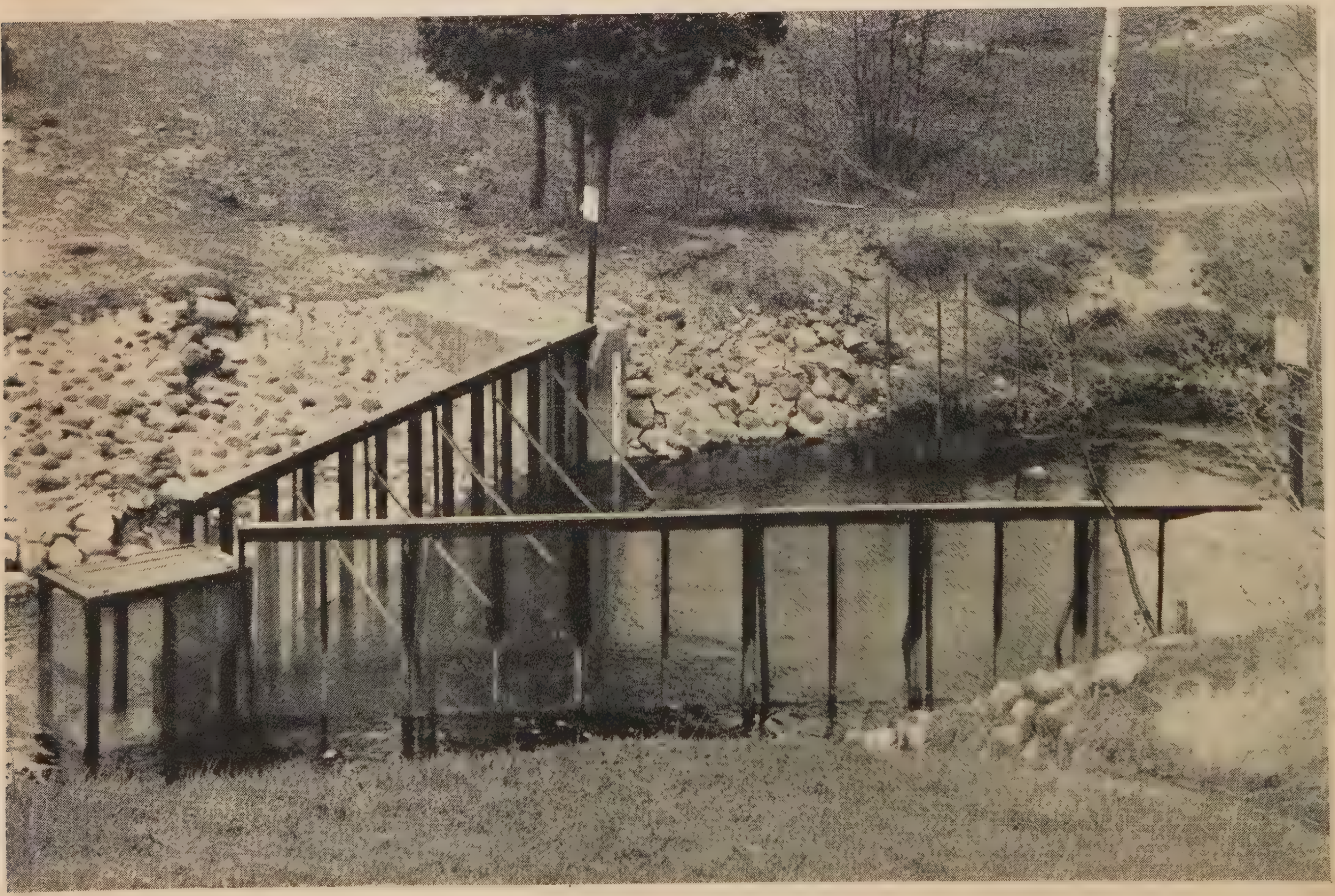
The adult lamprey apparently has a great range of movement. Marked lampreys, released in the autumn at the northern tip of Lake Huron, were recovered throughout the length and breadth of the lake by the following spring. Several individuals had traveled nearly the entire length of the lake, a distance of over 200 miles. But details of the lampreys' movements in the lakes are scanty. There is some evidence that they migrate first to deep water, where they attack lake trout, chubs and other deep-water species. As the lampreys grow larger, they move shoreward and in the fall are found in relatively shallow water. It is at this time that attacks on whitefish, suckers and other shallow-water fish reach their maximum.

Toward the end of winter sexually maturing lampreys begin to assemble off the mouths of streams. During this waiting period tremendous internal changes occur. The sex glands expand enormously, while the digestive tract shrinks and the lamprey becomes incapable of feeding. From now on it will live only on its own tissues. Even its muscles, skin and eyes deteriorate. If the lamprey is delayed in reaching its spawning grounds, death may overtake it before it can spawn.

Plainly the most vulnerable times in the lamprey's life are its periods in the stream—as a larva or young migrant and later when it goes back to spawn. The vulnerability is enhanced by the fact that only about 200 streams tributary to Lakes Huron, Michigan and Superior are suitable for spawning.

One attack on the lampreys has been to build mechanical weirs and traps and barrier dams to block their spawning runs. Although effective, these devices have numerous drawbacks. They are generally expensive to install and maintain; the weirs and traps must be cleared regularly. They may break down under flood conditions. The reproductive potential of the sea lamprey is so great that even a few escaping individuals can "seed" a stream sufficiently to maintain the population.

When the shortcomings of the me-



MECHANICAL WEIR crosses Carp Creek, a Michigan tributary of Lake Huron. It is designed to trap spawning lampreys as they go upstream. This kind of weir has been supplanted by electromechanical weirs such as the one depicted on the opposite page.

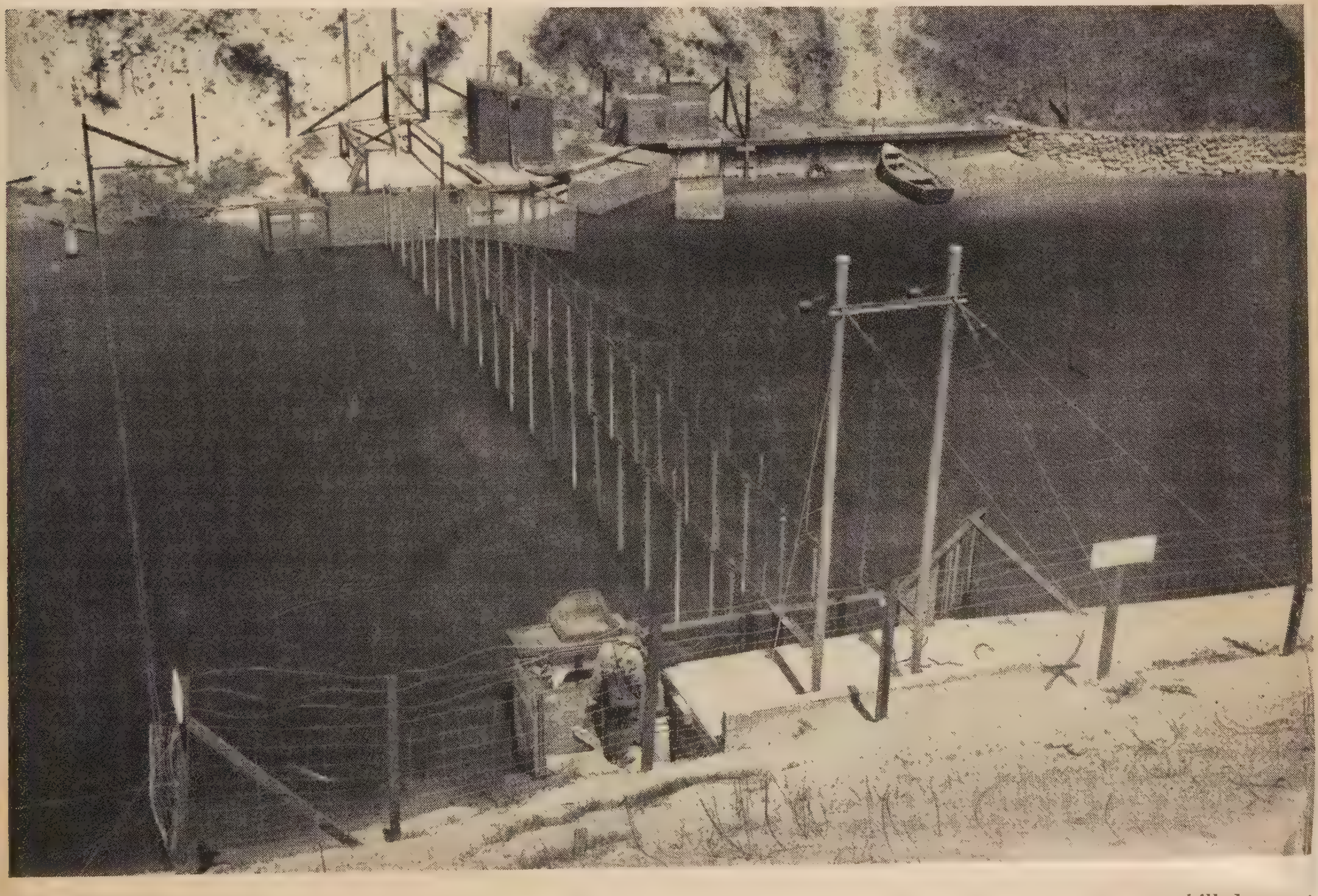
chanical barriers became evident, we turned to electricity. Linear arrays of electrodes were set up in the water to create electrical fields just strong enough to stop the movement of lampreys upstream to their spawning grounds. Using regular 110-volt alternating current, the electrical devices are more economical to construct and operate than purely mechanical structures. Unfortunately, however, the prevention of spawning, even if completely successful, will not show results for at least seven years. It will not kill off the generations of larvae already in the streams.

If we could destroy the larvae or the young downstream migrants, we might reduce the population substantially in less than two years. But so far no practicable means of achieving either objective has been found. Traps for capturing the downstream migrants do not work during the flood stages, when most migration occurs. A dam with an inclined-screen trap is effective, but it is expensive to build and requires continual attention. Furthermore, in many streams the topography precludes the use of this type of structure. Attempts were made to electrocute the young migrants with a simple system of electrodes in the stream, but these experiments were discontinued when it was discovered that young lampreys are extraordinarily resistant to electrical currents and the power required would be prohibitively costly. As for destroying the larvae, the problems become even more difficult. It was found that young American eels, a notably voracious species, would destroy lamprey larvae, but they kill desirable fish as well. So do most poisons. Recent investigations have, however, encouraged the hope that we may find chemicals which are toxic to lampreys and relatively harmless to other fish. Thousands of chemicals are being tested in an effort to discover a specific larvicide.

Notwithstanding the defects of the available control methods, the urgency of the Great Lakes fishing industry's plight has prompted us to apply some of them while better methods are being sought. Electromechanical barriers have been installed in 44 tributaries of Lake Superior on the U. S. side and 24 more are under construction in Canada. Practically all the spawning streams in the U. S. part of the Lake Superior basin have been blocked. In Lakes Michigan and Huron of course it is too late to save the trout. But if the trout can be protected in Lake Superior, they will provide a supply of eggs for restocking Michigan and Huron when the sea lamprey has been brought under control.

Fortunately no other fish has usurped the environmental niche of the trout in the Great Lakes. The small fishes on which trout feed have increased to the point of overcrowding, and there will be an abundance of food for trout when they can return. Another encouraging factor is that lampreys apparently do not single out trout if there are larger fish around. Thus when effective control of lamprey spawning comes into sight, we can begin to plant lake trout with the hope that the lamprey can be exterminated before the young trout grow large enough to be attacked. This may reduce the time required to develop a breeding population of trout from 11 years to seven.

Complete eradication of sea lampreys from the Great Lakes above Niagara Falls is our objective. It may prove to be a long operation, as difficult as the campaign sometimes necessary to stamp out an agricultural or forest pest, but we are confident that we shall ultimately succeed.



ELECTROMECHANICAL WEIR crosses the Ocqueoc River, also a Michigan tributary of Lake Huron. In the spring of 1954 10,183 lampreys on their way upstream to spawn were killed or captured at this site. No lampreys were found on the upstream side.

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NOTES ON THE CAPTURE OF YOUNG SAILFISH AND SWORDFISH IN THE GULF OF MEXICO.—Although the broadbill swordfish, *Xiphias gladius* Linnaeus, and the sailfishes, *Istiophorus* sp., are found throughout the warm waters of the world and are much sought-after game fishes, surprisingly little is known concerning their life histories. The following capture records of pre-adult forms taken in the Gulf of Mexico are presented as a contribution to our knowledge of these species.

Early stages of the swordfish are identified readily by referring to a series of excellent papers by Sanzo on the larval forms of this species. Identification of sailfish larvae poses a more difficult problem. As Voss pointed out in his recent paper on sailfish (1953, Bull. Mar. Sci. Gulf and Carib., 3 (3): 206–40), the very young of marlin and spearfish have never been taken to be recognized as such, and extreme care must be exercised to avoid possible confusion. With this possibility in mind, each specimen included in this presentation was compared and checked carefully with texts and figures in available publications on sailfish. Through the courtesy of Jack W. Gehringer, U. S. Fish and Wildlife Service, whose paper on the development of sailfish is now in preparation, they were compared and checked further with known sailfish specimens of similar sizes.

Plankton and dip-net collections made during field work aboard the M/V ALASKA and M/V OREGON, research vessels of the U. S. Fish and Wildlife Service, yielded fifteen larval and one juvenile sailfish, *Istiophorus americanus* (Cuvier), and thirty-two larval swordfish. The term "juvenile" refers to specimens in which metamorphosis into the general adult form has occurred, although several larval characteristics still may be evident. According to available literature, the ALASKA specimens, taken over the period from April 29, 1951, to June 19, 1953, were the first of the very young of these species to be captured in the Gulf of Mexico.

Capture records are given in Table I in chronological order. Standard length (S. L.) measurements are

TABLE I

CAPTURE RECORDS FOR YOUNG SAILFISH AND SWORDFISH

Under "gear", SN = ½-meter silk net,
Di = dipnet, MN = metal net

Species	S. L., mm.	Date	Time	Gear	Locality	
					N. Lat. °-'	W. Long. °-'
Sailfish	4.8	4/29/51	0900	SN	23–11	82–24
Sailfish	6.0	8/15/51	1400	SN	26–09	83–50
Sailfish	4.0	8/15/51	1400	SN	26–09	83–50
Swordfish	26.9	5/25/52	1012	Di	27–18	87–30
Swordfish	55.4	5/30/52	0015	Di	26–00	85–15
Sailfish	64.1	5/30/52	0015	Di	26–00	85–15
Swordfish	8.2	6/2/52	0600	MN	27–40	85–05
Swordfish	19.8	2/25/53	1030	MN	25–06	87–30
Sailfish	5.3	6/8/53	1945	MN	26–09	86–34
Sailfish	4.3	6/8/53	1945	MN	26–09	86–34
Sailfish	3.8	6/8/53	1945	MN	26–09	86–34
Sailfish	3.6	6/8/53	1945	MN	26–09	86–34
Swordfish	6.1	6/9/53	0500	MN	27–00	87–30
Sailfish	8.6	6/10/53	2100	MN	27–55	93–38
Sailfish	7.3	6/10/53	2100	MN	27–55	93–38
Sailfish	7.2	6/10/53	2100	MN	27–55	93–38
Sailfish	6.4	6/10/53	2100	MN	27–55	93–38
Sailfish	6.2	6/10/53	2100	MN	27–55	93–38
Sailfish	6.1	6/10/53	2100	MN	27–55	93–38
Sailfish	5.3	6/10/53	2100	MN	27–55	93–38
Sailfish	20–65	8/10 to 9/2/53	. . .	Di	. . .†	. . .†
Swordfish	79.5	5/8/54	Night	Di	26–40	92–00
Swordfish	49.1	5/8/54	Night	Di	26–40	92–00
Swordfish	51.5	5/10/54	Night	Di	24–22	92–00
Swordfish	34.2	5/10/54	Night	Di	24–22	92–00
Swordfish	47.0	5/21/54	Night	Di	20–25	95–45
Swordfish	28.0	5/22/54	Night	Di	21–42	95–35
Swordfish	47.0	5/23/54	Night	Di	22–10	96–20
Swordfish	43.2	5/23/54	Night	Di	22–10	96–20
Swordfish	42.9	5/23/54	Night	Di	22–10	96–20
Swordfish	42.5	5/23/54	Night	Di	22–10	96–20
Swordfish	38.2	5/23/54	Night	Di	22–10	96–20
Swordfish	28.5	5/23/54	Night	Di	22–10	96–20
Swordfish	51.0	5/24/54	Night	Di	22–30	96–57
Swordfish	50.5	5/24/54	Night	Di	22–30	96–57
Swordfish	50.0±*	5/24/54	Night	Di	22–30	96–57
Swordfish	39.5	5/24/54	Night	Di	22–30	96–57
Swordfish	39.0	5/24/54	Night	Di	22–30	96–57
Swordfish	37.3	5/24/54	Night	Di	22–30	96–57
Swordfish	35.0	5/24/54	Night	Di	22–30	96–57
Swordfish	32.5	5/24/54	Night	Di	22–30	96–57
Swordfish	32.5	5/24/54	Night	Di	22–30	96–57
Swordfish	49.5	5/26/54	Night	Di	24–00	96–50
Swordfish	20.2	5/26/54	Night	Di	24–00	96–50
Sailfish	. . .*	5/26/54	1400	MN	24–30	96–39
Swordfish	43.5	5/27/54	Night	Di	24–54	96–05
Swordfish	38.5	5/27/54	Night	Di	24–54	96–05
Swordfish	32.5	5/27/54.	Night	Di	24–54	96–05
Swordfish	?	5/15/53	Night	Di	21–45	81–45

* Specimen mutilated.
† Off Mississippi River delta (see text).

from the tip of the bill to the caudal end of the urostyle. Metal nets used for collection are high-speed plankton samplers (see Fish and Wildlife Service Special Scientific Report: Fisheries, No. 88). All specimens were taken either at, or within, five meters of the surface.

In addition to the foregoing collections, information concerning the capture of approximately 30 juvenile sailfish and one larval swordfish was furnished by Stewart Springer. The juvenile sailfish, ranging in length from about 20 to 65 mm., were taken by dipnet in August and September, 1953, during a cruise of the M/V Oregon, in an area extending from 28°50′ North, 88°50′ West to 29°10′ North, 88°00′ West, about 30 miles east southeast of the Mississippi Delta. The larval swordfish, although not taken in the Gulf of Mexico, was captured in such close proximity that its inclusion in this presentation seems justified.

These capture records strongly indicate that parts of the Gulf of Mexico serve as nursery grounds for sailfish and swordfish. In partial support of this contention, J. L. Baughman found that 17 out of 18 sailfish boated off Port Isabel, Texas, in August, 1940, had ova in all stages of development, and that several females taken later in the season had ova running from them (1941, Copeia (1): 33–7).

Although adult sailfish are taken regularly in the Gulf of Mexico, only three authentic records exist concerning the presence of swordfish above larval size in this area. On June 17, 1949, a dead specimen, estimated to be 12 to 14 feet in overall length, was found washed up on the beach of Padre Island, Texas, by Charles Urschel, Jr. (Kramer, 1950, Copeia (1): 65). A five-foot specimen (tip of lower bill to caudal fork) weighing 105 pounds was caught in Barataria Bay, Louisiana, on August 2, 1946, by Richard R. Foster, according to Harvey Bullis, of the U. S. Fish and Wildlife Service. On June 14, 1954, a 39-inch swordfish (tip of upper bill to caudal fork) was taken on a long line from the M/V Oregon, at a depth of ten fathoms, at 27°16′ North latitude, 90°25′ West longitude.—Edgar L. Arnold, Jr., *U. S. Fish and Wildlife Service, Galveston, Texas.*

SOME ASPECTS OF HOMING IN CUTTHROAT TROUT

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THE compulsion of an individual to return to a specific locality, usually for the purpose of reproduction, after a voluntary or involuntary absence, is termed the homing instinct. This phenomenon has been detected among certain vertebrate groups, such as mammals, fish, and, especially, birds. Fishery biologists have transposed the homing instinct into the parent stream theory. It has been shown to be a characteristic attribute of some migratory salmonoids, principally the Pacific salmon (*Oncorhynchus*) and the steelhead rainbow trout (*Salmo gairdneri gairdneri*). Briefly, this theory deals with the urge of a mature fish to return to the parent stream, where it had been liberated as a young fish, or hatched as the result of natural reproduction. Considerable literature is available pertaining to the homing tendency, its causes, occurrence, and significance, among these salmonoids. This literature has been adequately reviewed by Shapovalov (1941). A more recent publication of considerable significance relating in part to the quantitative aspects of homing in the silver salmon (*Oncorhynchus kisutch*) and the steelhead rainbow trout has been prepared by Shapovalov and Taft (1954).

While there can be little doubt concerning the positive existence of the instinct among these anadromous fish, adfluvial trout populations have received scant attention in this regard. Since 1949 the Rocky Mountain Investigation of the U. S. Fish and Wildlife Service has studied a population of this type in Yellowstone Lake, Wyoming. A single indigenous fish species, the Yellowstone blackspotted or cutthroat trout (*Salmo clarki lewsi*) inhabits this large alpine lake. It is the object of a large and successful sport fishery (Moore, Cope, and Beckwith 1952). In conjunction with an intensive research program which has featured creel census and tagging, a homing tendency has been detected among these fish and, in a sense, measured. It is noteworthy that this species and its anadromous counterpart (*Salmo clarki clarki*) have been largely avoided by fishery investigators as evidenced by the scarcity of published material about them. There is apparently a complete absence of literature regarding the validity and quantitative aspects of the parent stream theory for either species. Hence, this paper is intended first to be a contribution to our knowledge of the biology of the cutthroat trout in Yellowstone Lake by establishing the validity of the parent stream theory as it affects an adfluvial population. Secondly, the implications of this condition as it reflects upon the management of the species will be considered.

Yellowstone Lake (elevation 7,731 feet) is situated approximately in the center of Yellowstone National Park in Wyoming. It contains about 100 miles of shoreline and almost 90,000 surface acres. The cutthroat trout has been and is maintaining itself almost exclusively through natural reproduction. Each year during the late spring and early summer, sizeable spawning runs of mature fish ascend the various tributaries to the lake. The Fish and Wildlife Service has also operated fish traps near the mouths of several of the larger tributaries for many years. The purpose of this endeavor has been to obtain spawn from some of these wild fish for the hatchery and for distribution elsewhere. The balance of the runs have been allowed to ascend the stream and reproduce naturally. The cutthroat fry emerging from the gravels in the tributaries usually migrate into the lake within a relatively short period of time. There the greatest portion of the prematuration growth occurs. Those adults surviving the spawning rigors also disseminate back into the lake afterwards. The Rocky Mountain Investigation has directed much of the tagging activity at these gravid fish by utilizing the fish trap operations as collecting devices. In addition, a test stream was established in 1950, which has been devoted exclusively to experimental purposes. This tributary features a combination of upstream and downstream traps.

Data relating to homing by cutthroat trout have been gathered from two independent sources. First, the marking of lakeward bound immature fish was performed in 1950 and 1951 at the experimental stream. The young fish were obtained from the downstream trap and subjected to multiple fin clips. Some reappeared in the upstream trap after a period of several years as mature adults. This operation then measured the number of adults that returned to their parent stream from an original stock of immature fish. No account could be taken of those individuals which may have ascended tributaries other than those equipped with traps. Secondly, the tagging operation was conducted from 1949 through 1953 at the regularly trapped tributaries and the experimental stream. A tagged fish which re-entered the same tabulated as having homed back to the "parent" stream. Straying of tagged fish was detected only when they were present in the spawning runs of trap equipped streams other than the one in which they were tagged. Hence, this particular operation has provided a quantitative measure of the impulse of adult fish to return to the same spawning tributary following prior usage.

Previous to the present investigation, a fin clipping program was conducted at Yellowstone Lake by the U. S. Fish and Wildlife Service from 1940-1944. The specific purpose of this effort was to gather information regarding homing. A total of 43,009 small fingerlings averaging less than 2 inches in length were planted in three of the trapped streams during the marking period. The return of these marked fish was contemplated after several years of growth in the lake itself. The actual return of fin clipped fish as spawners thereafter proved to be inadequate and offered no assistance toward achieving the goal desired. Several factors contributed to the failure to obtain conclusive results. These factors are also important general considerations prerequisite for any marking program with this specific object being defined, and are listed as follows:

1. At the time of marking a systematic attempt to determine induced mortality from the fin clipping process, commonly called marking mortality, must be undertaken. This is particularly true where small fish are involved.

2. Multiple fin removal is more desirable than the amputation of a single fin. Since the natural loss or mutilation of a single fin (particularly the pectoral) in wild cutthroat trout occurs quite commonly, this technique would aid in the more positive identification of marked individuals. Furthermore, a fish with more than a single fin missing is much more readily recognized by an inexperienced or unobservant trap operator. The problem of attitude, effort, and the systematic maintenance of field records by the trap operators, especially when the detection of marked fish is incidental to enumeration and spawn taking, warrants serious consideration.

3. It is well known that salmonoids are notorious for their fin regeneration characteristics. This is owing both to the inherited susceptibility for certain fins to regenerate more than others, and to the fin clipping technique itself. Thus, consideration and care should be exercised in selecting the proper fins for such an experiment and in the fin removal process itself. A fin removed too close to the body could induce bleeding leading

to marked mortality, while a fin incompletely clipped may lead to excessive regeneration.

4. It should be recognized that some marked fish may return to streams other than those trapped. Homing studies have shown that some deviation from the inevitable return to the parent stream, designated as straying, can be expected. While it may be impossible to determine the complete extent of straying, care in the selection of the experimental stream in relation to neighboring tributaries may reduce the probability of a significant error in this regard. This observation was demonstrated and discussed by Shapovalov and Taft (1954).

5. An experiment of this type must be systematically carried through to its completion. It should be realized that the time and expense involved in the fin clipping of immature fish necessitate thorough and complete enumeration of subsequent trap returns thereafter. More effort extended over a longer period of time must be obligated to obtain the marked fish returns than was put forth for the actual fin clipping process itself.

The results obtained from the fin clipping operation at the experimental stream in 1950 and 1951 have been arranged in table 1. These data indicate that a strong tendency for these fish to return to their parent stream does exist. From 16 to 25 percent of those young fish marked as one year olds returned as three and four year adults. With due regard for the imposition of natural and fishing mortalities during the period of prespawning lake residence, it appears that a minimum amount of wandering into untrapped tributaries must have taken place. No instance of fin clipped adults venturing into other trapped streams has been noted.

Table 1. *The return of marked immature cutthroat trout to the parent stream*

Year marked	Size class	Probable age	Number marked	Trap returns			
				1951	1952	1953	1954
	millimeters						
1950	51-90	1	224	–	47	9	5
1951	51-90	1	236	–	–	26	12
1951	41-140	2	184	–	16	6	7

The return of spawners to each of the six tributaries having trap installations has provided additional quantitative insight into the homing urge among cutthroat trout. From the 17,836 adult fish tagged at these trap sites (1949-1953), 280 individuals have again appeared as repeat spawners in the same tributary where originally enumerated. During the same period of time, only 6 tagged fish classified as repeat spawners were counted in the other streams. This is a minimum rate of straying amounting to approximately 2 percent. In addition, predictions of the expected number of mature fish that should reappear in the "parent" stream which were based on adult mortality estimates have consistently agreed within reasonable limits with the actual returns.

The evidence, therefore, is somewhat conclusive, although not in a strict quantitative sense, that a homing instinct does exist to a rather high degree among cutthroat trout in Yellowstone Lake. Not only does this impulse compel the fish to return to their parent stream for initial spawning, but occasions a return to that stream thereafter for repeat spawnings. This latter condition is particularly meaningful because of the intervening variable of lake dispersion between spawnings. The validity of the parent stream theory for an adfluvial lake population implies that immature trout present in Yellowstone Lake are predestined to return to specific spawning tributaries at the time of maturity. The predetermination has been established by the early life stream association, in this case as the result of natural reproduction.

The practical implications of the parent stream theory reflects upon a management program. This is especially true of a lake whose stock of fish is dependent upon natural reproduction, or on the take of spawn from wild fish which thereafter may be planted back into the lake system. A spawning run into a particular tributary could be destroyed, or almost completely obliterated by not allowing a sufficient escapement past a trap or fishery for natural spawning. In lieu of an adequate escapement, a stream must receive an ample plant of eggs or fry in order to maintain the run. The regulation of the opening date of the sport fishery with respect to the spawning runs is another means of insuring additional escapement to the spawning areas.

What, then, is the presumptive fate of planted cutthroat trout in the lake proper? Being out of the influence of the tributary, it is well to contemplate where they will return as gravid adults. Will they return to the area in the lake where the plant was made, and, being unable to spawn successfully, represent a complete loss in reproductive potential? Will they migrate at random to tributaries through the lake, or possibly, to a stream most proximal to the area where they were planted? Obviously, the answer is not available.

However, since the planting of salmonoids in lakes is quite often practiced in order to take advantage of productive feeding areas, it is of utmost importance to consider the significance of the homing instinct in relation to a management plan for that particular body of water. It is hoped that in the near future the Rocky Mountain Investigation will be in a position to shed some additional light upon this complex and important problem.

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SELECTIVE SETTING OF OYSTER LARVAE ON ARTIFICIAL CULTCH

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The consistently high oyster spatfall in the Gulf area sets this region apart from many other areas where oysters are cultured. Since knowledge of the causes of success or failure of a set is of great importance to the industry, we initiated studies on this problem at the Pensacola Laboratory in 1949. We made systematic counts of the time and frequency of spatfall in conjunction with continuous records of hydrographic conditions. This paper presents some of the general conclusions derived from a study of five years of data, especially those relating to larval behavior at the setting stage.

It was necessary to select materials and methods for this study which would permit comparable results over a period of years and not be cumbersome. The collection of spat on oyster shells while having many desirable features has also some obvious objections, especially the difficulty of computing the exposure area. For this reason, several flat artificial materials were tested with the results shown in Figure 1. We sanded the surface of the Plexiglas so its texture was comparable to the other materials used. The fact that spat avoided the white Plexiglas is obviously not due to a color reaction, since the rates on black are nearly as low whereas the rate on white oyster shell is very high. We examined only the white surfaces of the oyster shells and carefully computed the area of the exposed surfaces, so that these data could be expressed as rates per square centimeter. The cement board, which received the highest set, is that commonly used for building purposes. It is easily handled and costs approximately one cent per 4 inch square plate. Such a plate provides one hundred square centimeters of exposed surface. We also tested smooth and rough surfaces and found over a long period that each receives the same amount of set. Since the smooth surface of the cement board is so much easier to examine, it is the only one we used routinely.

In the five years of observations, we have never had a routine plate, that is one exposed for 7 days, without at least one sedentary animal form. We have had concentrations of oysters as high as 30 per square centimeter; that is roughly comparable to a set of 700,000 per bushel of shell. Barnacle rates have at times been over 100 per square centimeter. In general, when the concentration of a species reaches 0.5 per cm^2 or more, counting 10% of the surface provides an accurate index of the total set. When oyster concentrations were below this figure, we examined from one to four full plates each week. We wash the plates under a strong jet of water before examination so that any debris or animals not firmly attached will be removed.

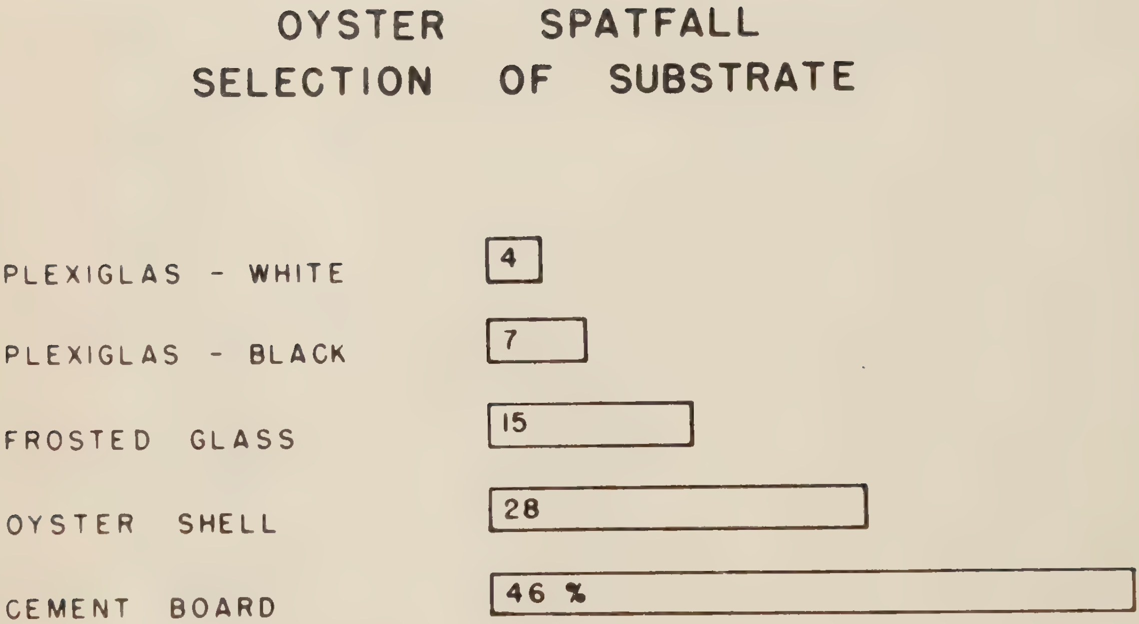


Fig. 1. Percentage occurrence of spat on plates of different materials exposed for 7 days. Plates were exposed simultaneously and adjacent to each other. Data include approximately 3,000 oysters.

Figure 2 shows the rack containing cement board plates which is exposed each week throughout the year. In special studies, other racks of similar nature carried plates at different angles. The racks hang halfway between surface and bottom in three meters of water on one of our docks. Figure 3 shows a horizontal rack carrying different colored plates about $1\frac{1}{2}$ meters below the water surface. This photograph indicates the usual clarity of the water during the oyster spawning season.

One of the first things noted in our examinations was the preponderance of spat on the upper surface of exposed plates. Figure 4 shows the relative numbers of spat setting on upper and lower surfaces of plates exposed throughout the setting season for four years. I have included here similar data on barnacles because of their probable correlation with the data on oysters.

This figure also shows the daily incidence of oyster spat on upper and lower surfaces of plates exposed for limited periods. Dark plates were exposed from 7:30 P.M. until 3:30 A.M. on consecutive moonless nights, while light plates were in full sun from 7:30 A.M. until 3:30 P.M. on the intervening days. These data are somewhat limited and the experiment will be repeated next summer, but it appears that the majority of setting in this area occurs in daylight hours and on upper surfaces.

Since the weekly plates are exposed at mid water level, we determined the relative frequency of set at different levels in our area. Figure 5 shows the percentage of the total set which occurs at one foot intervals below mean low water. The first series, held on a fixed rack, shows approximately one per cent of the set occurring at the surface and nearly 80 per cent confined to the 4 - 7 foot levels. We repeated this work using a floating rack which fluctuated with the tide and obtained very similar results. The slight variations in numbers setting on the lower plates in the second series are of no real significance.

In the third series, we extended the rack so the last plate was a scant inch above the bottom. This experiment showed a very different picture as to the location of the oyster set. Nearly 50 per cent of the set was on the bottom plate.

The disparity between our data and reports in the literature led us to repeat some of the experiments first reported by A. E. Hopkins in his work on the Olympia oyster in 1935. Figure 6 shows the incidence of set on plates held at different angles in the water. These plates were in separate racks but exposed simultaneously for 7 day periods. Again, as on our other plates, we found the majority, 78 per cent, setting on upper surfaces (135° plus 180°) and only 18 per cent on lower surfaces. These data were difficult to reconcile with Hopkins' results which are shown on the third line of the table. More than 86 per cent of the Olympic oyster set occurs on under surfaces and less than one-half per cent on the upper surface.

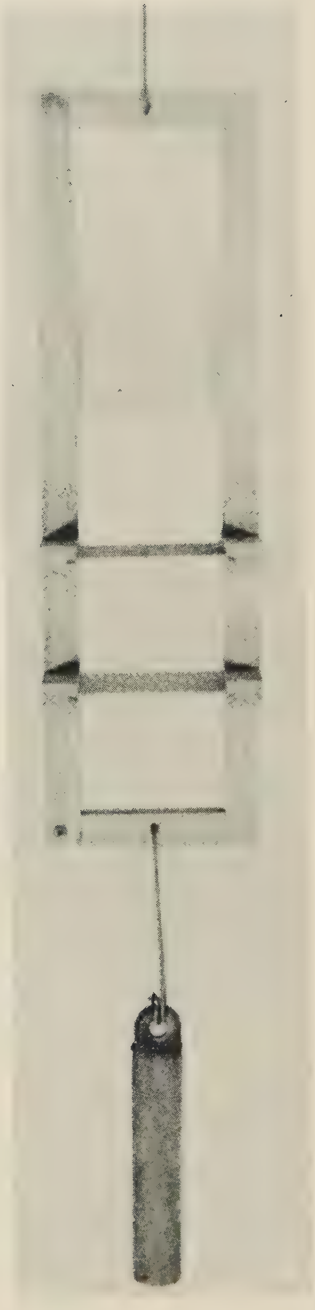


Fig. 2. Weighted wood rack with four inch square asbestos cement board plates. Each plate surface provides 100 cm^2 area for attachment of sedentary organisms.

Fig. 3. Photograph of rack carrying white, transparent, and black plates $1\frac{1}{2}$ meters below water surface.

OYSTER SPATFALL SELECTION OF SURFACE

4 - YEAR AVERAGE

	UNDER	UPPER
OYSTER	36 ± 4	64 ± 4
BARNACLE	57 ± 5	43 ± 5

DAILY INCIDENCE %

	UNDER	UPPER	BOTH
DARK	40	60	26
LIGHT	43	57	74

Fig. 4. Percentage of oysters and barnacles setting on upper and under surfaces of cement board plates throughout spawning season for four years. Data include approximately 70,000 oysters and twice as many barnacles. Daily incidence of setting shows percentage of oysters found on upper and under plates exposed for 8 hour periods of continuous darkness or light.

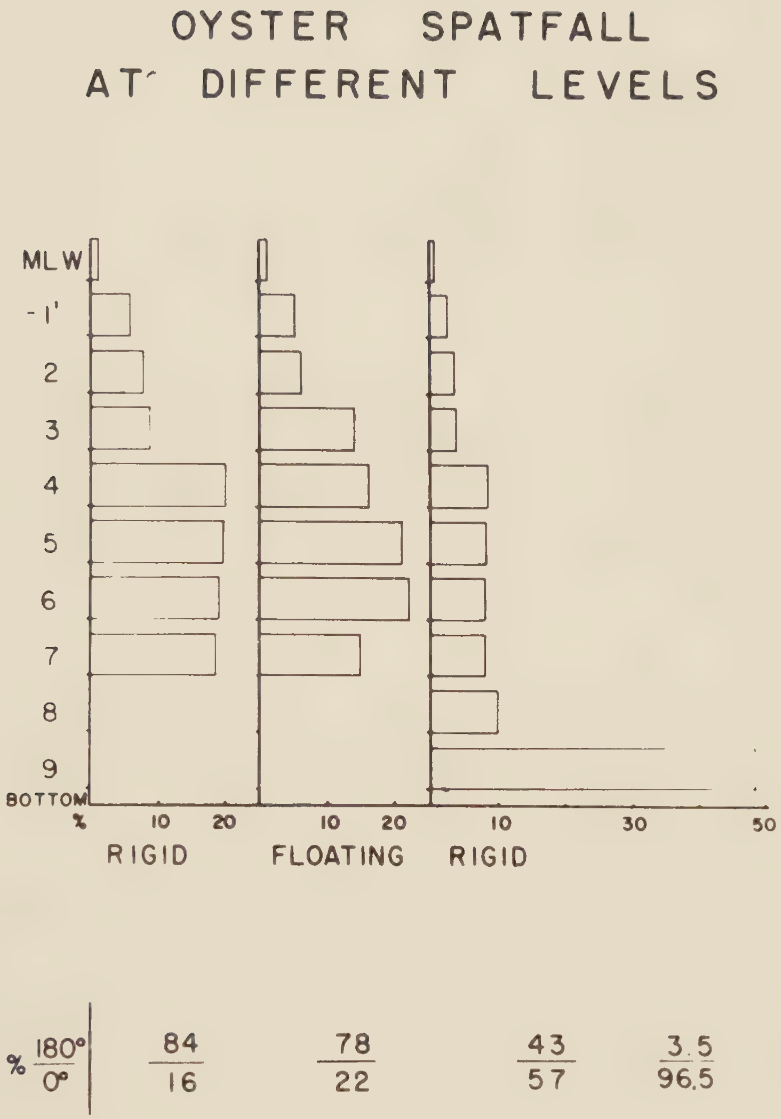
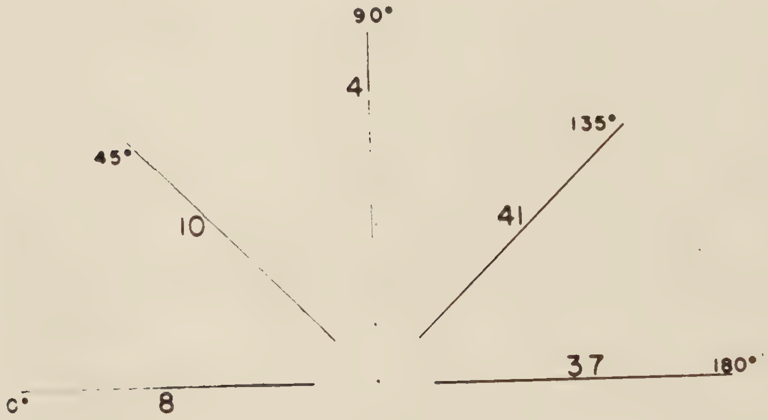


Fig. 5. Percentage of oysters setting on both surfaces of horizontal plates held in rack at one foot intervals. Racks were fastened to wharf (rigid) or suspended from float which fluctuated with the tide. Ratios show percentage of oysters setting on upper (180°) and under surfaces. Last ratio indicates plate at 9 foot level.

OYSTER SPATFALL
ANGLE OF INCIDENCE - %



	0°	45	90	135	180
SUSPENDED	8	10	4	41	37
ON BOTTOM	96.6				3.4
ON BOTTOM	86	13	.7	.2	.1-
SUSPENDED	70.5	15.5	5.5	6	2

Fig. 6. Percentage of oysters setting on cement board plates held at several angles. Data include approximately 6,000 oysters. Tabulation compares results obtained at Pensacola (first two series) with results obtained by other investigators.

We find the answer to these apparently conflicting results by referring again briefly to Figure 5. As noted earlier, 50 per cent of the set in the third series occurs on the bottom plate, but more significantly, 96 per cent of these are on the under surface of the bottom plate. On all of the remaining plates, the majority of the set occurs on the upper surfaces. The ratio of top to bottom set for each series is shown in the lower part of the figure. The last ratio is that of the bottom plate of the third series.

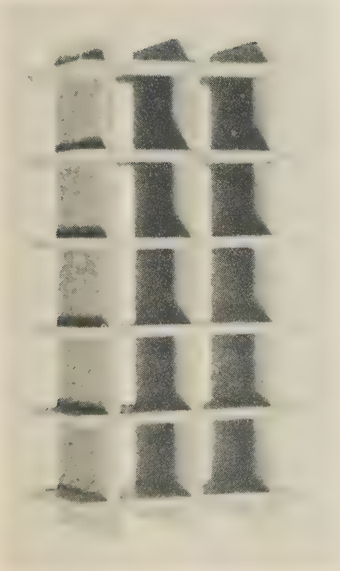
If we examine Figure 6 again, we find reasonably good agreement between my plates and Hopkins' plates which were located on the bottom. The final line in the table indicates the data obtained by a third investigator using frosted glass plates suspended above the bottom. These data include all bivalves but were primarily oysters. The results are in good agreement with Hopkins' but are almost the exact opposite of my own data shown on the first line of the table. This was especially interesting to me, since Dr. Pomerat did this work at Pensacola in 1940.

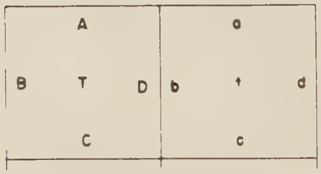
We repeated his experiment as closely as possible, using the same locations and, perhaps, some of the identical glass plates which he used, but are unable to confirm his observations. Since our results have been consistent over the past three seasons, I conclude that some special hydrographic feature was present during the two weeks that he conducted his experiment. Possibly in 1940 excessive turbidity caused a rapid sedimentation of his plates preventing bivalves from setting on the upper surfaces.

Figure 7 shows one of the special crate collectors used to compare spatfall here with other areas where crate collectors have been tested. Each cubicle of the crate measures approximately 2 x 2 x 4 inches. We find this type of cultch expecially efficient in attracting oyster spat, as many other investigators have reported. I have tabulated the actual numbers of spat counted in a single test. The uniformity of these numbers, depending on the angle of surface, is extremely interesting. Various organisms covered only about 10 per cent of the surfaces of the plates and hence there was very little competition for attachment space. The fact that each section in the crate caught nearly identical numbers of oysters indicates to me an unexpectedly uniform dispersion of larvae in the plankton. The percentages of oysters found on the different surfaces of all of these collectors agree with results obtained on plates held singly and in series.

From these and other experiments I gain a general picture of the behavior of oyster larvae at the setting stage in the Pensacola area. The greatest deterrent to setting is a layer of sediment, just as in other areas investigated. A deposit of silt only as deep as the larvae, about 1/75 of an inch, will prevent their attachment on what is normally a preferred surface and cause them to set on a surface they would ordinarily avoid. The larvae have no particular attraction for black or white

OYSTER SPATFALL - CRATE COLLECTOR





NUMBER ON ONE CRATE

A -	20	a -	27
B -	19	b -	19
C -	255	c -	257
D -	32	d -	31
T -	326	t -	334

PERCENTAGE BY ANGLE OF SURFACE

	EXPERIMENTAL	CONTROL
0°	6	20
90°	16	10
180°	78	70

Fig. 7. Photograph of cement board "crate collector" and tabulation of setting on inner surfaces of the ten cubicles. Lettered diagram designates surface positions; T - t indicates sum of all surfaces in each vertical row of cubicles. Collectors were suspended at mid depth in three meters of water for seven day periods. Data include approximately 5,000 oysters.

backgrounds either in the dark or daylight hours, and when above the bottom have little preference to the lighted or unlighted side of a plate. I find no evidence that phototaxis plays a part in their selection of cultch.

In one limited series of experiments, the larvae set primarily during the daylight hours. They appear to set equally on the rising and falling tides as well as during slack water periods. This may be a special condition of the Gulf environment, where there is only one tide each day and the change in water level is slight.

We can predict the location of the spat, other conditions being comparable, almost entirely on the basis of the larvae's struggle against the laws of gravity. The majority are located and set on the bottom and their numbers decrease as the distance from the bottom increases. As the larvae swim upwards through the water they are just as likely to hit and set on an under surface as, when they fall back down through the water, they may hit and set on an upper surface. I believe there is no relation bwtween the swimming position of the larvae, i.e. with its foot upwards, and the surface on which the larva attaches.

There are two factors of prime importance in determining the utilization of a surface as cultch. Sediment physically interferes with setting on upper surfaces; this factor increases in importance near the bottom where currents that might wash silt away are relatively weak. The second factor of importance is the occurrence of barnacles. Barnacles may set more quickly than oysters on newly exposed cultch and the sweeping action of their appendages in collecting food repels the larvae. On upper surfaces, this sweeping action does not interfere too much with larvae which drift down between the barnacles and set. On vertical and under surfaces, however, when an oyster larva comes into contact with this field of activity it closes and falls away from the surface. Relatively few barnacles can seriously interfere with the setting rates on vertical and under surfaces. In all of our work we have found that deviations from the expected 1:1 ratio of spat on upper and under surfaces can be correlated with the numbers of barnacles on the under side. Barnacles have a marked preference for setting on under surfaces, and this leads to the predominance of the oyster set on upper surfaces in this area. The importance of barnacles is obscured or overshadowed on bottom cultch where siltation is of paramount importance.

In summarizing this work, it appears that in this area the movement of mature larvae is governed almost entirely by the laws of chance and gravity. The only selectivity larvae show in setting results from their avoiding silt or other organisms and they will be found on the first clean surface they can reach regardless of its position in the water. It should be noted that these data refer to the incidence of setting and not spat survival. In some areas, factors causing early mortalities operate at certain levels or positions. This condition may produce an erroneous picture of the original location of the spatfall.

POSSIBLE CAUSES OF GROWTH VARIATIONS IN CLAM LARVAE

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In recent years advances in larval research have greatly increased the possibility of raising the hard clam, Venus mercenaria, under hatchery conditions. As the commercial cultivation of clams becomes increasingly feasible, numerous questions are raised about all its phases. Perhaps the most frequent questions concern the causes for differences in the rate of growth of larvae. These causes may be those brought about by environmental differences and those that are inherited.

The effect of variation of environmental factors on the rate of growth of larvae has been studied to some extent. Thus, the effects of variations in temperature, density of population, and the type and quantity of food have been reported (Loosanoff, Miller and Smith, 1951; Carriker, 1952; Loosanoff, Davis and Chanley, 1953a; Loosanoff, Davis and Chanley, 1953b; Loosanoff and Davis, 1953). However, very little is known about inherited variations. Loosanoff, Davis and Chanley (1953c) reported that, in general, there was no relationship between the age or size of the parent and either the size of the larvae or the viability of the spawn. They also reported that variations in both the viability of the spawn and the size of the larvae were common. Individual differences in larval size, within the same culture, have also been observed on many occasions (Loosanoff and Davis, 1950; Marak, 1951; Davis, 1953). Since environmental conditions for all larvae, within the same culture, should be virtually identical, some of these variations must be caused by inherited differences.

This study was designed to evaluate some of the effects of inherited factors on the growth and survival of clam larvae. It should be emphasized, however, that this report presents the results of preliminary studies and, therefore, the conclusions are tentative and may need to be revised in the future.

In the first experiment we compared the larvae from several combinations of parents to determine the influence of each parent on the rate of growth of the larvae. Three female and three male Venus mercenaria were induced to spawn in the laboratory by increasing the water temperature and adding millipore filtered sperm water. The eggs of one female (3) were then divided into three groups and each group was fertilized by the sperm of a different male. This resulted in the crosses - 3 x 1, 3 x 2, and 3 x 3. Sperm from 1 was also used to fertilize the eggs of the other two females (1 and 2), giving the crosses 1 x 1 and 2 x 1. Triplicate cultures from each cross were then started, using approximately equal numbers of eggs, in 18 liter earthenware culture jars. These jars were kept in a common water bath to minimize the temperature differences between the cultures. During

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the course of the experiment the temperature ranged from 19.0° to 22.1°C. but at no time did the maximum temperature difference between the jars exceed 0.7°C. All cultures were fed equal quantities of Chlorella daily. Water in the jars was changed and larval samples taken at two day intervals.

On the second day, after fertilization, a count was made to determine the percentage of eggs that had developed to normal straight hinge larvae and the population in each culture was then adjusted to approximately 180,000 to 200,000 larvae. The percentage of survival and the number of cultures continued for each cross are shown in Table I.

Several factors were probably responsible for the differences in the percentages of eggs that developed normally into straight hinge larvae. The length of time between the discharge of spawn and fertilization may be cited as an example. We have found that the percentage of developing eggs decreased rapidly as the time interval between spawning and fertilization increased. This was apparently caused by the loss of viability of the sperm since another sample of the same eggs showed a high percentage of development if fresh sperm were used. Since the first male spawned more than two hours earlier than the last female, it is possible that the differences in survival in some of these crosses were partially due to the differences in the age of the sperm at fertilization.

It is also possible that mechanical damage may result from screening or transferring the eggs after cleavage has begun. This may be responsible for some of the abnormalities and lower rates of survival in this experiment, since some of the eggs had undergone cell division before all the cultures could be started.

These factors cannot account for all the observed differences, however, for in the 1 x 1 cross the sperm was fresh and the same sperm, used later in the day, initiated good development in the eggs of 2 and 3. Moreover, the eggs in the 1 x 1 cross were handled soon after fertilization and the cultures were started before cleavage had begun. Nevertheless, such a small percentage of the eggs developed to normal straight hinge larvae that the cultures of this cross were discarded. Since this female spawned very lightly while the other clams spawned more heavily, it seems reasonable to suspect that the condition of the eggs was responsible for their poor development. Possibly the eggs were immature. Davis (1949) reported the release of immature eggs by oysters and Loosanoff and Davis (1950) stated that, "Probably some clams were compelled by the strong temperature stimulation to abort the eggs even if the eggs were not fully ripe." on the other hand, clams can retain mature gametes for extended periods of time without the loss of viability. Loosanoff and Davis (1951) found that normal larvae could be raised even when the gametes were not released until several months after the end of the normal spawning period.

Table I. Number of fertilized eggs used in each cross, percentage developing to normal straight hinge larvae, and number of cultures continued for growth studies.

CROSS	TOTAL Eggs Cultured	TOTAL Normal Larvae At 2 Days	PERCENTAGE Of Normal Larvae	NUMBER Of Cultures Continued
1 x 1	753,000	--	less than 10	0
2 x 1	1,638,000	672,000	45	3
3 x 1	1,500,000	942,000	63	3
3 x 2	1,500,000	360,760	24	2
3 x 3	1,500,000	180,000	12	1

When two females were crossed with the same male, 2 x 1 and 3 x 1, there was a significant difference in the size of the larvae at two days (Fig. 1). Significance was determined by the use of the "t" test. The "t" value was 13.014, consequently the probability was much less than .001. However, from the second day to the conclusion of the experiment, this difference in larval size remained constant and consequently the growth rates were nearly identical. Since no similar difference in larval size at two days was recorded when one female was crossed with three males and since the rate of growth, after the second day, was nearly equal in all crosses of this experiment, it seems unlikely that any inherited difference in rate of growth was responsible for the difference in size of the 2 x 1 and 3 x 1 larvae at two days. We may conclude, therefore, that significant differences in the size of the larvae at two days are caused primarily by some factor, such as the size of the egg. Such a concludion is, however, tentative since at present we have only limited data on the correlation of egg size with the larval size at two days.

There was a considerable range in size within each culture although all the larvae within a single culture were from the same parents. This size range increased with the age of the culture, as can be seen by comparing the length-frequency distribution of larvae at two days with that of the same larvae at ten days (Fig. 2). Apparently, then, certain individuals grew consistently faster or slower than average, although the environment must have been virtually identical for all larvae within a culture. Although the effect of possible environmental differences, within a culture, cannot be entirely eliminated, the range in length, observed in these crosses, must have been at least in part due to inherited differences. It would seem, then, that even among sibling larvae, there is a wide range of inherited differences that affects the rate of growth.

In a repeat experiment stripped sperm were used so that all sperm would be approximately the same age at fertilization. All eggs were placed in jars before cleavage had begun, to avoid damaging the early embryos by screening. Temperatures ranged from 22.8° to 24.3°C. with a maximum difference of 0.4°C. between jars at any given time. On the second day, populations were reduced to about 150,000 larvae per jar. Otherwise, the procedure employed was the same as in the first experiment.

In the stripping process, the body fluids of the male are unavoidably mixed with the sperm. It is not known how these fluids affect the gametes or the developing zygotes. Some workers (Just, 1939) have demonstrated that, in other species, the body fluids interfere with the normal development of the eggs. This danger was probably slight in our experiment, since the water containing the eggs and sperm was greatly diluted when the eggs were put in culture jars. These fluids

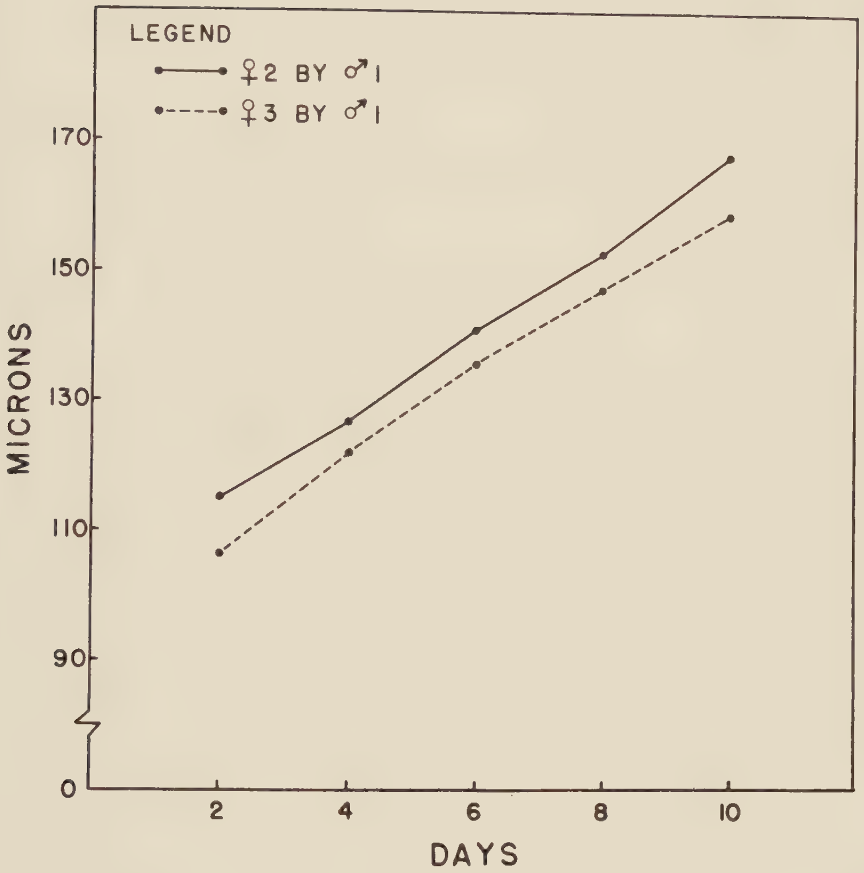

Fig. 1. Growth rates of larvae from two different females crossed with the same male. Each point represents the mean length of 100 larvae from each of triplicate cultures.

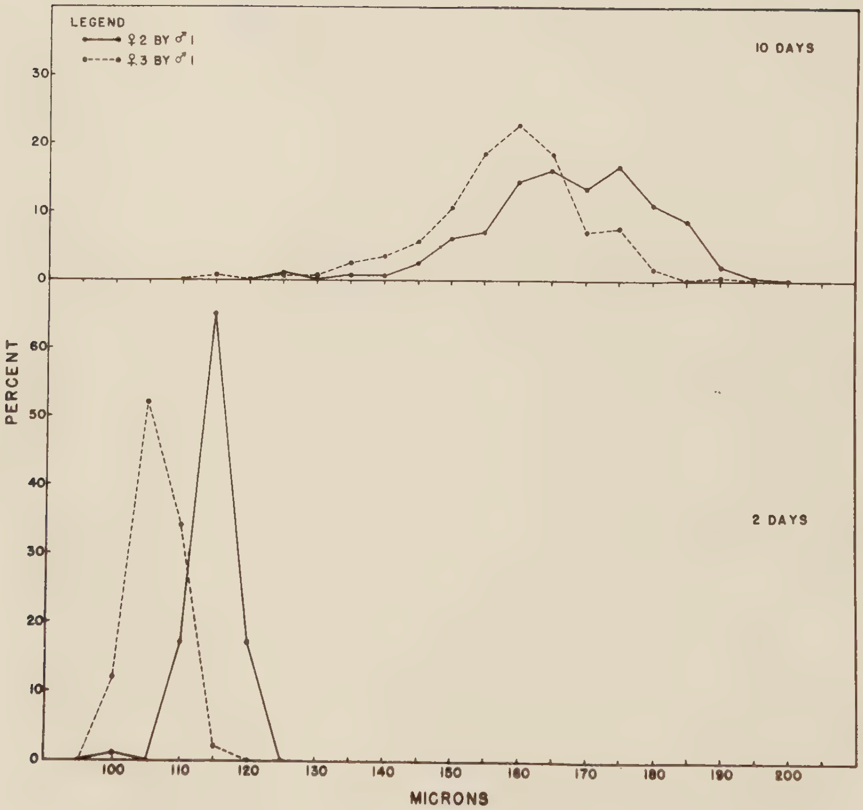

Fig. 2. Length-frequency distribution of the same two crosses at two and ten days showing the increase in range with the age of the larvae.

should not, in any event, have had any effect on the larvae after the water was changed on the second day.

The numbers of larvae were not equal in all cultures for the first two days. There is no reason to believe that this affected the percentage of eggs developing to the normal straight hinge stage since the heaviest concentration was no higher than in many other experiments in which the development was normal. Nor is there any reason to believe that this affected their growth during the first two days since there was no appreciable difference in the size of the straight hinge larvae with the possible exception of the larvae from the B x A cross. The larvae of this cross were somewhat smaller but so few developed that they were discarded. Triplicate cultures of the A x A and A x C crosses, duplicate cultures of the A x B cross, and a single culture of the C x A cross were continued for growth rate studies. The differences in the percentage of eggs that developed normally must be primarily due to the condition of the eggs in this experiment.

The larvae from the C x A cross grew more slowly than those from the A x A cross (Fig. 3), and by the sixth day the difference was statistically significant, that is, the 95% confidence limits did not overlap. Since the growth rates of these crosses were different throughout the experiment, the difference appears to have been caused by factors inherited from the female parent. The differences in rates of growth, when one female was crossed with three males, were not nearly as pronounced. However, the difference between the mean lengths of the larvae from the A x A and the A x B crosses gradually increased and by the tenth day the 95% confidence limits determined statistical significance. (Fig. 4). This difference must have been the result of inherited influences of the male parent. The mean lengths of the larvae from the A x C cross are not significantly different from either the mean lengths of the A x A or the A x B larvae.

I would like to express my appreciation to Dr. V. L. Loosanoff and Mr. H. C. Davis for their invaluable assistance in all phases of the work. I am also indebted to Miss R. S. Riccio and Mr. C. A. Nomejko for their assistance in the preparation of the manuscript.

SUMMARY

1. Significantly different rates of growth were found between larvae from the same female crossed with two different males and also between larvae from two separate females crossed with the same male. It is tentatively concluded that inherited differences from either of the parents may be responsible for these differences in the rate of growth.

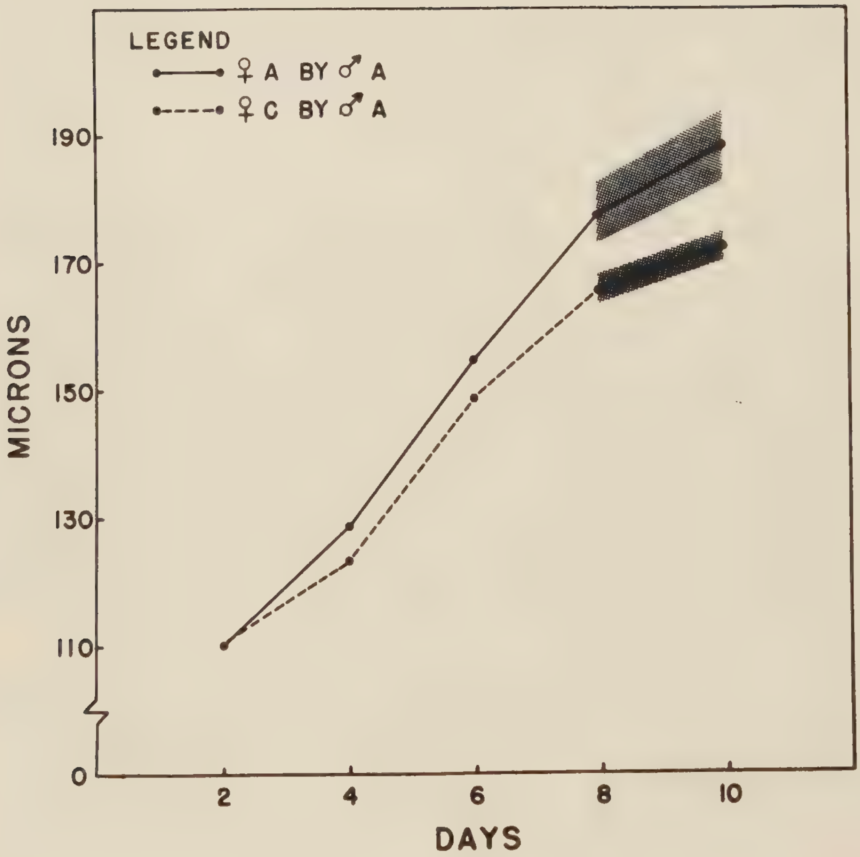

Fig. 3. Growth rates of larvae from two different females crossed with the same male. Points on the ♀A x ♂A line are mean lengths of 100 larvae from each of triplicate cultures. Points on the ♀C x ♂A line are mean lengths of 100 larvae from a single culture. Shaded areas are the 95 per cent confidence limits.

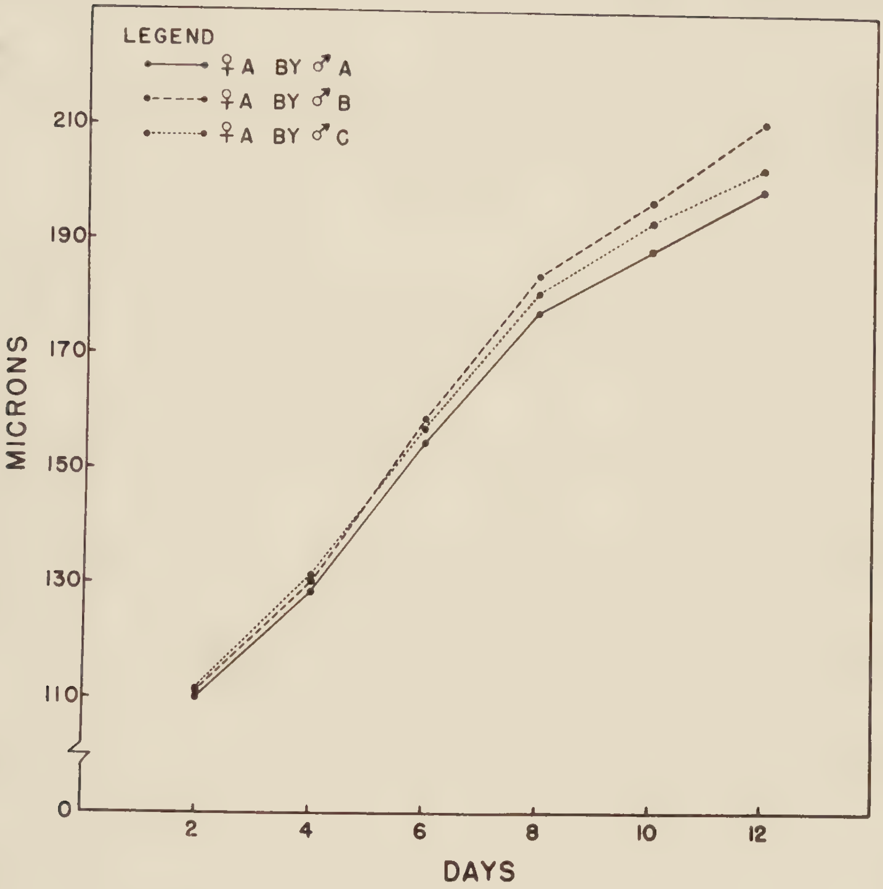

Fig. 4. Growth rates of larvae from a single female crossed with three males. Each point on the ♀A x ♂A and ♀A x ♂C lines represents the mean length of 100 larvae from each of triplicate cultures. Each point on the ♀A x ♂B line represents the mean length of 100 larvae from each of duplicate cultures.

2. Significant differences in the mean lengths of larvae at two days were not correlated with subsequent differences in growth rate. It is tentatively concluded that these early differences are caused by physiological differences in the eggs.

3. The range of length of larvae, from a single pair of parents, increased as the larvae grew larger and older. Apparently, then, sibling larvae have widely different rates of growth. At least part of this difference is believed to be a result of inherited differences.

4. The ability of sperm to fertilize eggs decreases as the time between the discharge of sperm and fertilization increases. Eggs remain fertilizable for a longer period of time.

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THE FUTURE OF THE CUTTHROAT IN UTAH

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THE explorers and naturalists who invaded the Intermountain Region in the 1870's and 1880's for the purpose of finding and cataloging the flora and fauna of the territory encountered one species of trout in the Rocky Mountains. This trout, observed in many color patterns in various drainages, was given many specific and subspecific names by taxonomists, but we now recognize that the several forms were all cutthroat trout (*Salmo clarki*), a fish popularly and appropriately known in this area as the "native" trout. Despite the fact that introductions of many species of exotic trout have been made into the Intermountain Region, and that the native cutthroat have been taken elsewhere for stocking, the cutthroat has been recognized as the trout of this region. Trends and events of recent years seem, however, to have conspired to threaten the fate of the cutthroat in many parts of the Rocky Mountain empire. Perhaps in no other state is the threat as serious as in Utah. This state has featured the cutthroat as one of its most important sport, and even commercial, fish since before the report by Yarrow (1874) of red-throated trout in Utah Lake weighing 15½ pounds and measuring three feet in length. This paper will attempt to show what has transpired in Utah to change the outlook for this species, and to reveal how some factors are interrelated.

The fishery for cutthroat in Utah before 1900 was almost wholly dependent upon natural reproduction for the replenishment of populations. Although the total amount of trout spawning gravel in Utah is considered to be somewhat limited, the available spawning space was probably reasonably efficiently utilized. It is a matter of record that sizeable cutthroat migrations occurred from Utah Lake into its tributaries each spring, and that many other waters in the state (Bear, Sevier, Duchesne Rivers) supported moderately large populations of cutthroat.

Fish-cultural work in Utah began in 1872, when the U. S. Fish Commission inaugurated a program for the propagation and distribution of food fishes. From this time until the turn of the

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century there was much activity in the area of introducing exotic species of fish into Utah and of planting barren waters. Importation of cutthroat trout into Utah for supplementing natural populations and stocking new waters had its start during this period, and was intensified after 1900. The early construction of hatcheries in Utah gave impetus to the program of importation of cutthroat as well as to the practice of culturing eggs collected within the state. In the year 1915, 1,977,500 cutthroat were planted in Utah waters, as well as 7,703,000 fish of other species, most of which were trout. Of the cutthroat stocked in 1915, 100,000 were imported from outside the state to supplement local egg collections. These trends in cutthroat stocking and the receipt of eggs from outside the state persisted through the years in response to the requirements of increased fishing, and in the biennium 1950-1952, 10,657,578 fry and fingerling cutthroat were planted from the 12 hatcheries of the state of Utah and the federal hatchery at Springville. From 1915 to 1952, 33 percent of all the fish stocked in Utah were cutthroat. Of these planted cutthroat, numbering 111,986,588 fish, 45 percent were brought from outside the state, and almost exclusively from one source, Yellowstone Lake.

Concurrent with this growth in fish cultural activity in Utah, and directly relating to it, an increase in fishing pressure was taking place. It is impossible to obtain an accurate index of fishing pressure and fishing success for the state as a whole during this period, but an examination of fishing and hunting license sales will reveal the trends that occurred. In 1907 there were approximately 20,000 fishing and hunting licenses sold in Utah. This number increased to 100,000 in 1938 and growth was even faster in the next 15 years. There were 208,890 licenses issued in the year 1953 in the state.

The cutthroat trout in Utah had achieved the following status by 1950: It was at least the second most popular game fish in the state. Its original representatives, the Utah cutthroat and the Colorado cutthroat, had been largely if not completely replaced by the Yellowstone cutthroat. Importations of Yellowstone cutthroat had been stocked not only in many barren waters in the state, but in most other waters suitable for the species. The hatchery program had grown in response to increases in fishing pressure, and heavy stocking of trout was the practice. A third of all fish planted in the state were cutthroat trout, and almost half of the planted cutthroat were introduced from out of state.

Even prior to 1953 at a time when the cutthroat program in Utah was flourishing, management practices were being modified.

The continuation of these altered fish management methods, in combination with engineering developments and other trends, had placed the future of cutthroat in jeopardy. Let us look for an explanation of the processes at work and a prediction of the fate of the species in Utah.

The first of three threats to the welfare of cutthroat to be felt in Utah was the blocking of spawning runs by the construction of dams. Damage to cutthroat migrations began many years ago with the development of engineering works on streams. The famous cutthroat of Utah Lake were denied access to their tributary spawning gravels by early irrigation developments and by subsequent installations in the same vicinity. There now exist 6 or more dams on the streams entering Utah Lake. Three of these are on the Provo River, one on Spanish Fork River, one on Salt Creek, and one on Hobble Creek. At least one more dam is proposed for the Provo River and others on tributary streams. The cutthroat of Utah Lake have disappeared almost completely, and dams on tributary streams are responsible for a large share of this loss. Similar blocking of spawning migrations has already been accomplished in others of the five principal drainages of Utah. In the Bonneville Basin several dams have been built. In the Weber Basin several structures are already operating on the Ogden and Weber Rivers. The Bear River, a stream that held cutthroat years ago, no longer contains them in their former abundance. In the Colorado Basin, Scofield and Strawberry Reservoirs are established.

The dams already in existence in Utah have had their effect on the spawning of cutthroat in years past. Perhaps of greater import at the moment are the plans for future irrigation and power development in the Colorado River Basin. Plans are now projected for new dams in the central Utah drainages, lying in the Colorado and Bonneville Basins. The territory in which the greatest potential for detrimental effects on cutthroat migration may occur is along the south face of the Uinta Mountains. This relatively remote region is potentially one of the richest recreational areas in Utah, and contains some of the best cutthroat populations in the state. By virtue of its popularity as a fishing area the loss of the Uinta Mountain streams will be severely felt in Utah when dams are built. The plan for the development of this area calls for diversion structures on each major stream from Brush Creek, near the Colorado boundary, westward to the headwaters of the Strawberry River and involving approximately 25 diversions.

A second threat to Utah's cutthroat lies in the introduction of rainbow trout. When cutthroat and rainbow are established in a stream the two species ordinarily distribute themselves so that the cutthroat occupy the more boreal habitat and the rainbow reside in the downstream stretches. Artificial fish distribution usually has been carried on with this principle in mind, and rainbow plants have not ordinarily been made into waters occupied by cutthroat. There has been a recent trend in many western states toward the stocking of rainbow into cutthroat waters. Such stocking modifies the species composition and this becomes intensified because of the readiness with which these two species hybridize in nature. When rainbow-cutthroat hybridization occurs in the wild, the rainbow stock seems to dominate over the cutthroat, and the cutthroat strain diminishes or disappears.

The chief reason for the tendency in Utah to place more and more rainbow in cutthroat water stems from the necessity of providing fishing for more fishermen. Great emphasis is placed on the stocking of legal-sized trout, a practice which seems to be necessary where there is heavy fishing pressure in waters with mediocre natural reproduction. Rainbow trout can be much more easily and inexpensively reared to legal size than can cutthroat. The experience in most places has been that high mortalities occur in cutthroat hatcheries, so the rainbow is the preferred trout for culture to catchable size. The natural result has been a greater emphasis on planting of large rainbow trout in cutthroat streams as well as in waters more suited to rainbow.

The third factor that may seriously influence the abundance of cutthroat in Utah is the instability of the supply of eggs for culture. It was noted above that the state was decidedly dependent upon Yellowstone Lake for cutthroat eggs from year to year, with almost half of the cutthroat planted in Utah originating from this one source. Recent changes in the management of the fishery on Yellowstone Lake by the National Park Service have curtailed the supply of eggs for use outside of Yellowstone National Park. Utah received no Yellowstone eggs in 1954, and the prospects for a revival of acquisitions in the near future appear to be poor. The state of Utah is thus faced with the alternative of developing of new brood stocks of cutthroat within the state, or making replacement with one or more other species. The probable course will be an augmentation of the use of rainbow to fill the gap.

History shows that increasing numbers of obstacles have been faced by the cutthroat trout in Utah in its struggle for prevalence. The two original subspecies of cutthroat were replaced by a third, which flourished under the management conditions in effect until recently. The influences of water control structures in streams have rendered spawning more difficult. The curtailment of nearly half of the egg supply of former years has resulted in an even greater reliance on the rainbow to meet the needs of heavy fishing pressure. The introduction of rainbow into cutthroat waters has further limited the space available for the native fish. The prospects for the future of the cutthroat in Utah would seem to be poor in view of the fact that some of the influences discussed here will be increased in the future. The cutthroat will be exposed to even greater hazards in the attempt to retain its important place as a game fish in Utah. This trout, the only native species of trout in Utah, will not be entirely eliminated from the waters of the state, but it is not expected to ever again occupy the dominant place it once held.

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MORTALITY OF OLYMPIA OYSTERS AT LOW TEMPERATURES

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The ability, or inability, of organisms to become acclimated to a new environment becomes economically important when, for example, it is desired to increase the number of oysters or clams in a given area by transplanting seed oysters or clams from a different geographical area. It is also of importance when trying to establish oysters or clams in areas where they do not now exist.

In the fall of 1948 a shipment of Olympia oysters, *Ostrea lurida,* was brought to Milford, Connecticut from Puget Sound for experiments with their larvae. This shipment was divided into two groups. The group that was kept suspended in Milford Harbor, which freezes in winter, suffered 100 per cent mortality.

The second group kept in the laboratory, in running sea water at temperatures above 10.0° C., survived the winter and later provided the larvae for our experiments. The larvae were reared to metamorphosis and the young oysters reached a size of 3.5 to 3.7 cm. some 70 days later (Davis, 1949). Since oysters that set in April or May become sexually mature by the following spring, if protected during the winter, we were able to maintain our experimental stock by rearing a new generation every year.

Records, from the fall of 1948 through the winter of 1954–55, show that in Milford Harbor the water temperature, quite regularly, remains below 10.0° C. from some time in November until the end of April, and ranges from 5.0° C. to −1.0° C. from mid-December until the end of March. To prevent a complete loss of our Olympia oysters, through winter killing, it was necessary to bring some of them into the laboratory between mid-December and mid-January each year.

During the winter of 1948–49 the Olympia oysters that suffered 100 per cent mortality had been below the ice, in wire baskets suspended from floats. Those kept in Milford Harbor during the winters of 1949–50, 1950–51, and 1951–52, were under similar conditions and, while detailed records were not maintained, only those kept in the laboratory throughout the winter survived. In 1952–53 we had one of our outdoor tanks covered to prevent freezing. Although the temperature in this tank was approximately the same as in Milford Harbor, no ice formed. The Olympia oysters left in this tank all winter, nevertheless, showed 100 per cent mortality (Table I).

The following winter (1953–54) 101 Olympia oysters of the 1952 year-class, and 160 from the 1953 year-class, were left in hatchery-type tanks of running sea water in our unheated dockhouse throughout the winter where, again, no ice formed. An additional 834 from the 1953 year-class were brought into the laboratory about mid-January. One group of 528 of the latter was kept in unheated running sea water at a temperature that rarely rose above 5.0° to 10.0° and occasionally dropped to 3.0° or 4.0° C., while the remaining 306 were kept in running sea water at about 10.0° to 12.0° C. The group kept at 10.0° to 12.0° C. suffered appreciably less mortality than the other group kept in the laboratory at the lower temperature, and the latter group in turn suffered less mortality than those left in the dockhouse all winter (Table I). It was suspected, however, that much of the mortality in both laboratory groups was a continuation of the winter mortality that was already apparent in the dockhouse before these oysters were brought in.

During the winter of 1954–55 Olympia oysters of the 1954 year-class were suspended from the dock well below the ice line. About mid-December, before any mortality was apparent, 191 of these oysters were brought into the laboratory and kept at about 12.0° C., while the remaining 625 Olympia oysters were left suspended from the dock all winter. When these two groups of oysters were examined March 30, 1955, only seven, or 3.6 per cent, of those at 12.0° C. were dead and at least two had probably died of shell injuries. The 625 oysters left suspended from the dock, however, were all dead by March 30.

TABLE I

Winter mortality of O. lurida at Milford Laboratory under different conditions

Year	Place oysters were kept	Number of oysters	Per cent mortality
1948–49	Suspended from float; under ice	Several hundred	100.0
1949–50 1950–51 1951–52	Suspended from float; under ice	Several hundred	100.0
1952–53	Baskets in covered outdoor tank; lowest temp. −0.7° C.	Several hundred	100.0
1953–54	Dockhouse; lowest temp. −0.7° C.	1952 set—101 1953 set—160	100.0 100.0
	Laboratory; 5.0–10.0° C. or lower	1953 set—528	86.74
	Laboratory; 12.0–13.0° C.	1953 set—306	60.50
1954–55	Suspended from dock; below ice	1954 set—625	100.0
	Laboratory; 12.0–13.0° C.	1954 set—191	3.6

Since death usually occurs only after a month or more of exposure to low temperature, it might be assumed that it was the result of a depletion of stored food brought about by the prolonged period of water temperatures below their feeding temperature. This does not appear to be the explanation, however, since a majority of the dying oysters still contained a good reserve of glycogen.

Loosanoff and Nomejko (1951) have found that even oysters of the same species, *Crassostrea virginica,* as our Long Island Sound oysters, namely, oysters from North Carolina and Florida, suffered 87.0 per cent and 97.0 per cent winter mortality when kept in Milford Harbor. They also found that *C. virginica* from Virginia and also from nearby New Jersey did not become completely acclimated, even after two years in Long Island Sound, as shown by their failure to spawn.

Conversely, Loosanoff (1951, 1955) has shown that the European oyster, *Ostrea edulis,* a larviparous oyster closely related to *O. lurida* and belonging to the same genus, could not only survive in American waters but could reproduce as far north as Maine.

Imai *et al.* (1954) reported that seed oysters, produced from *O. lurida* imported to Japan, "all died of freezing" during the winter of 1950 at Mangoku-Ura. In 1954 they had seed oysters at Saroma, Usu and Onagawa Bays and state that the mortality of *O. lurida* was nearly twice as high as for the native Japanese oyster at each bed. Moreover, their data seem to indicate that the mortality of *O. lurida* increased progressively from Onagawa, in the south, to Saroma, their most northern station. Thus, their observations closely parallel our 1953–54 data which showed progressively increasing mortality as the temperature at which *O. lurida* was kept was decreased.

Our observations indicate that the winter mortality of Olympia oysters in Milford Harbor results from an inability to withstand prolonged exposure to low temperatures, and that this inability is inherited. Our breeding stock was selected each year, to the extent that the oysters used to rear a new generation were brought into the laboratory only after the least resistant had already succumbed to the low water temperature in the harbor. Nevertheless, even after five generations at Milford, Olympia oysters have still not become acclimated to the prolonged low temperatures of our winters.

The author wishes to express his appreciation to Dr. V. L. Loosanoff, Director of Milford Laboratory, for his continued interest and counsel in this project.

SUMMARY

1. Olympia oysters, kept throughout the winter in Milford Harbor, showed 100 per cent mortality.

2. The mortality of these oysters increased progressively as the temperature at which they were kept was progressively decreased.

3. Death usually occurred after a month or more of exposure to low temperatures.

4. Mortality did not appear to be due to tissue starvation, since many of the dying oysters still contained a good reserve of glycogen.

5. Although our breeding stock was selected, each year, after the least resistant oysters had already succumbed, Olympia oysters, even after five generations at Milford, had still not become acclimated to our prolonged period of low temperatures.

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A FUNGUS DISEASE IN BIVALVE LARVAE

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The method for growing bivalve larvae as now practiced at the U. S. Fish and Wildlife Service Laboratory, Milford, Connecticut, has offered many new possibilities for studying the behavior and physiological and ecological requirements of these organisms (Loosanoff, 1945; Loosanoff and Davis, 1950). Using this method larvae of 16 species of bivalves have been successfully cultured through metamorphosis. Of these, however, the larvae of the common clam, Venus mercenaria, and of the American oyster, Crassostrea virginica, have received the most attention (Loosanoff, Miller, and Smith, 1951; Davis, 1953).

Because of their hardiness and simpler dietary requirements clam larvae are especially suitable for experimental work and their cultures have been reared through metamorphosis as a matter of routine. On several occasions, however, some cultures of an experimental series would show a heavy mortality unrelated to the experimental treatment. In the spring of 1953, while examining such a culture of clam larvae, we noticed an organism, which was tentatively identified as a fungus, in many of the dead or dying larvae. We later observed the same or a related fungus in larvae of C. virginica, Venus mortoni, and the hybrids of V. mortoni x V. mercenaria and V. mercenaria x V. mortoni.

In both clam and oyster larvae the fungus may develop as a thallus of limited extent occupying a relatively small part of the larva so that its form and structure can readily be seen (Fig. 1, A, B, C). In contrast, in many of the specimens of invaded clam larvae there is a much more extensive growth, the fungus occupying a large proportion of the space within the larval shell with its lobes or segments so densely crowded together in a radiate arrangement that the details of thallus organization cannot readily be discerned (Fig. 1, D). It has not yet been determined whether this difference in thallus character indicates that the simpler, less extensive growth represents a younger phase which may later develop into the more elaborate one or signifies that two different species of fungi are concerned.

With either type of thallus as the fungus develops, the segments mature into sporangia, each with an exit tube extending to the exterior (Fig. 1, D). The zoospores, which develop fully and become motile within the sporangium, emerge through these tubes into the surrounding water. In some cases these tubes appear to become excessively elongated and extend for some distance beyond the larval shell (Fig. 1, E).

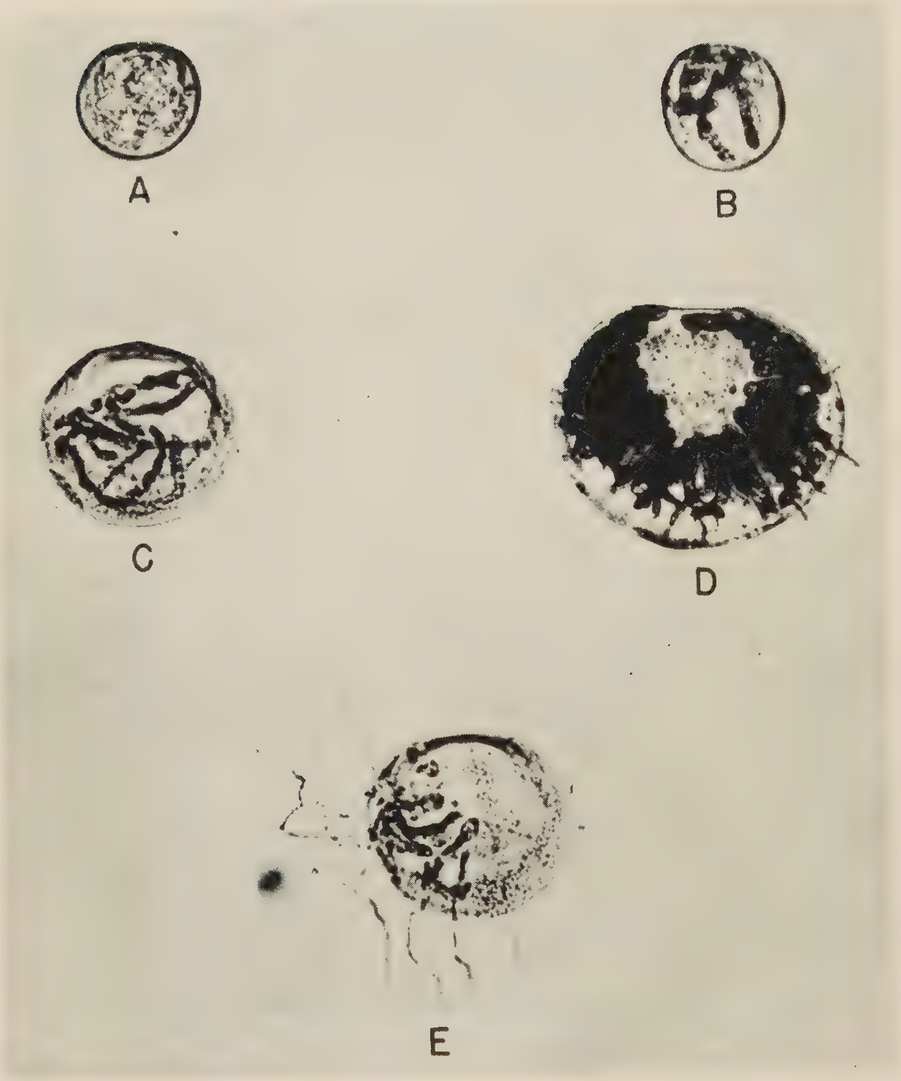

Fig. 1. Larvae infested with fungus. A and B, young oyster larvae; C, young clam larva; D, old clam larva; E, young clam larva. Larvae A, B, C, and E are stained with Neutral Red; larva D, with Cotton Blue. Magnification 190 times.

No sexual stage of the fungus, nor any resting spores or other resistant bodies have yet been observed.

The fungus is transmitted by the zoospores which emerge through the tip of the exist tube. These zoospores are released in an intermittent stream and are frequently seen for a short time in a swarm near the edge of the shells of the larva from which they have escaped, but soon disperse throughout the water. Theoretically densely crowded larval cultures should present a better opportunity for development of fungus epidemics than would field conditions because the larvae are so crowded that it must be almost impossible for them to avoid taking in some of the zoospores released into the water by infected larvae.

The presence of fungus in our larval cultures usually was of endemic nature, i.e., there were a few infected larvae in many of the cultures. Only in a few instances did the disease acquire epidemic proportions involving the majority of the larvae and, within two to four days, killing almost the entire population.

During the course of an epidemic many larvae were observed in various stages of disintegration with the fungus quite apparent inside the shell. Usually several species of flagellates and ciliates invaded the dead or dying larvae to feed upon their tissues leaving, within a short time, empty shells with practically no trace of the fungus. Rapid disappearance of the tissues made it very easy, in certain instances, to overlook the fungus which caused the mortality. The zoospores are very small and early hyphae are not readily visible. It may be significant that even in those cultures in which mortality was especially severe there were usually some larvae that lived through the epidemic without contracting the disease. The presence of these individuals raises the question as to whether some larvae are immune to the fungus.

Larvae of all ages, from the very early free swimming stage to those ready to metamorphose, have been found parasitized by the fungus. Also on several occasions we have observed juvenile clams, just after metamorphosis, that were heavily infested and releasing fungus zoospores.

At present we do not know the optimum salinity or temperature for the growth of the fungus nor the limits it can withstand. The larval cultures in which the fungus has been observed have all been in our normal sea water which has a salinity of about 27.0 parts per thousand, and have been kept at constant temperatures between 19.0 and 27.0°C. Nor do we know whether some infected larvae may survive the infection, recover from it and proceed with normal development. In a few instances we have observed the fungus in larvae that were still capable of swimming about. It seems, however, that the majority of the larvae drop to the bottom, stop growing, and die soon after they become infected.

Dr. Weston and Mr. Martin of the Biological Laboratories, Harvard University have tentatively identified the fungus as Sirolpidium sp. among the lower members of the biflagellate series of Phycomycetes. Although its thallus is similar to Lagenidium calinectes, which is known to cause similar destructive epidemics among the larvae of the blue crab in Chesapeake Bay (Couch, 1942), the maturation and release of zoospores are completely different and affiliate our fungus most closely with the genus Sirolpidium. The two known species within the genus Sirolpidium, however, while both parasitic and both marine, have only been reported on such algae as Bryopsis and Ceramium and have never been found on animal hosts. The indications are, therefore, that these fungi attacking clam and oyster larvae represent one or perhaps even two new species.

We have found that if living larvae are placed in a weak solution of Neutral Red in sea water, the fungus acquires a distinct reddish color and becomes easily distinguishable. The method is promising not only as a practical way to demonstrate the presence of the fungus, but also as a help in detecting its first appearance. By "tagging" the infected larvae it may permit us to determine how long fungus infected larvae can survive, whether they grow, and answer other pertinent questions arising in the course of an epidemic.

Although we have not yet been able to obtain and test the new fungi-static antibiotic oligomycin, isolated by Dr. Elizabeth McCoy et al. at the University of Wisconsin, we have attempted to find other methods for controlling this fungus. Since it remains endemic in many of our cultures, or may disappear after killing only a small percentage of the larvae, it is difficult to be certain that any given treatment is effective in reducing the death rate from fungus. However, as the motile zoospore stage is presumably the most susceptible to poisons, we have concluded that a treatment is ineffective if motile zoospores are found following the treatment.

By this criterion the fungicidal stains Fast Green and Malachite Green were found to be ineffective both when the larvae were dipped in the stain for periods up to ten minutes in concentrations as great as one part of stain to 15,000 parts of sea water and when the stain was added to the culture jars in concentrations up to one part per million. Bursoline, a fungicide developed for the Pacific Theater of World War II, was also found to be ineffective.

Copper sulfate was ineffective in killing the zoospores even when added to cultures in concentrations of one part per 100,000. Many clam larvae survived six days of treatment in this high concentration of copper sulfate although they remained relatively inactive during this period. In contrast, oyster larvae were killed by concentrations of copper sulfate as low as one part per million and the culture jars in which copper sulfate had been used required several washings before they lost their toxicity for oyster larvae.

Ultraviolet irradiation of larval cultures was ineffective in doses up to four hours per day. Fluorescent sunlamp irradiation up to seven hours per day did not rid the cultures of the fungus but continuous irradiation killed the clam larvae and appeared to sterilize a culture killing everything including bacteria.

We believe this is the first report of a fungus parasite in bivalve larvae, and only a few parasitic fungi have been reported in marine animals. This discovery may indicate, therefore, that parasites and diseases of bivalve larvae may be more destructive in nature than heretofore thought. It is also possible that this fungus may be responsible for the heavy mortalities sometimes observed in nature among clam and oyster set, for it has killed almost every young clam in one of our laboratory trays that contained several thousand recently metamorphosed clams. Moreover, there is the possibility that such an epidemic among bivalve larvae in nature could upset the balance of events in the food chain and thus affect other species. If we can develop a method for control of this fungus under laboratory conditions, the artificial cultivation of certain bivalves may soon be commercially feasible.

We wish to express our thanks to our colleague, Mr. C. A. Nomejko, for making the photographs for this article and to Miss Rita Riccio for her assistance in editing and preparing the manuscript.

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THE REPRODUCTION OF LAKE TROUT IN SOUTHERN LAKE SUPERIOR

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Abstract

The principal spawning grounds of lake trout (*Salvelinus namaycush namaycush*) in United States waters of southern Lake Superior are on rocky shoals at depths of less than 20 fathoms. Most spawning occurs in October and early November. Of the mature fish collected on or near the spawning grounds, 60 to 69 percent were males. Among mature fish the average length of females was greater than that of males; few males less than 24 inches or females less than 26 inches in total length were caught. Recoveries of lake trout tagged on the spawning grounds showed that some males remained in the immediate area for a period of several weeks during the spawning season. Marked fish showed a tendency to return during later years to spawning grounds on which they had been tagged, even though many of them ranged long distances between spawning seasons.

The percentage of the total weight composed by gonads of maturing females collected in 1950 was 5.0 percent on August 11–30 and 12.3 percent on October 6–9, but this increase was not accompanied by an increase in the coefficient of condition.

One volumetric and two gravimetric methods for estimating numbers of eggs in ovaries were evaluated. Some advantage in accuracy of estimate resulted from the drying of eggs in an oven before weighing on an analytical balance. Production of eggs by 70 lake trout ranging from 25.1 to 38.0 inches in total length and from 5.8 to 19.6 pounds in weight ranged from 2,476 to 17,119. Average production was 646 per pound of fish; this number was greater among fish 31.0 inches long or larger than for fish of smaller size.

Thirteen fish identified by commercial fishermen as siscowets (*Salvelinus namaycush siscowet*) also showed extensive individual variation in numbers of eggs, although egg production tended to increase with increasing length and weight of the fish. A mature female siscowet as small as 16.5 inches long and a 15.7-inch mature male were collected about 45 miles north of Grand Marais, Michigan. Combined data from all collections showed that spawning of lake trout or siscowets may occur during at least 6 months of the year (June to November).

Introduction

Materials for the study of certain aspects of the reproduction of lake trout in Lake Superior were provided by collections from commercial catches and from experimental gill nets, by recoveries of sexually mature fish which had been tagged on their spawning grounds, and by related field observations, during the years 1950–1954. Although some material from other regions is included, the data are restricted largely to the Marquette-Munising district of south-central Lake Superior. It is believed that this geographical restriction has helped to limit the collections to a single race

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or to closely similar races typical of this region, thus avoiding possible confusing effects of physiological differences among the several races of lake trout which are recognized by commercial fishermen (Van Oosten, 1944). Data are added in the last section on reproduction of the siscowet.

Collecting stations and other localities of special interest to which reference is made in the text and tables are shown in Figure 1. Also shown is the boundary of statistical district S–4, one of six geographical areas used in the analysis of commercial fishery statistics of State of Michigan waters of Lake Superior (Hile, Eschmeyer, and Lunger, 1951), within which most of the data were collected.

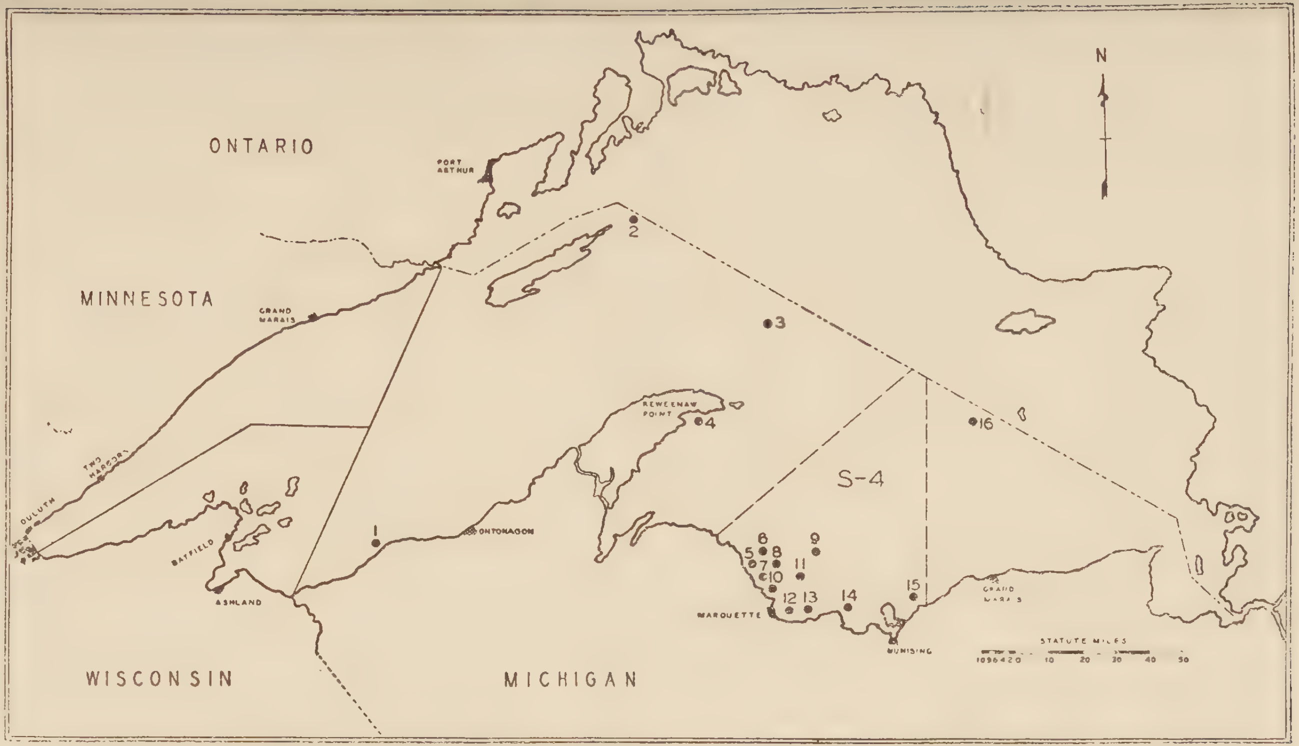
Some of the field collections on which this paper is based were made by Leo F. Erkkila, in charge of the Marquette, Michigan, station of Great Lakes Fishery Investigations, Fish and Wildlife Service. Joseph Beil, Clifford Tetzloff, and W. S. Glidden assisted in work in the field. Further aid was given by William E. Gladfelter in the laboratory work and by George F. Lunger in the statistical analysis of the data. James W. Moffett and Ralph Hile read the manuscript and offered suggestions. William Cristanelli prepared the illustrations.

SPAWNING GROUNDS AND SEASON

The principal lake trout spawning grounds in United States waters of southern Lake Superior are widely distributed on rocky shoals, at depths of less than 20 fathoms. The main evidence of their location is the concentration in the vicinity of these grounds of sexually mature fish before and during the spawning season, as revealed by increased catches in gill nets of the commercial fishery and the occurrence in these catches of ripe or nearly ripe fish.

There are no published records to date of direct observation of spawning fish in southern Lake Superior, and it is doubtful whether they commonly spawn in water sufficiently shallow to be observed from the surface. Such observations were attempted during two spawning seasons, off Keweenaw Point in October 1950 and near Marquette in October 1953, during periods when the presence of some ripe fish in the general area was shown by their capture in nets. Waters of shoreward areas with rocky bottoms were cruised with a skiff and the bottom observed with a spotlight during evening hours when observations in other waters (Merriman, 1935; Royce, 1951) would indicate that spawning fish might be expected. No lake trout were observed during either year, although a few fish of other species (believed to be round whitefish, *Coregonus cylindraceus*, and burbot, *Lota lota*) were seen in the Marquette area.

In addition to the occurrence of ripe fish in gill-net catches, other evidence of the location of spawning grounds was obtained off Marquette (Station 10, Fig. 1) in March 1953 when 2 recently hatched lake trout (yolk-sac stage) and 1 lake trout egg (in addition to many eggs and fry, presumed to be coregonines, and cottids and invertebrates) were collected during limited use of an apparatus devised for the purpose. This gear


N
ONTARIO
PORT ARTHUR
MINNESOTA
GRAND MARAIS
TWO HARBORS
DULUTH
BAYFIELD
ASHLAND
WISCONSIN
MICHIGAN
ONTONAGON
KEWEENAW POINT
MARQUETTE
MUNISING
GRAND MARAIS
S-4
1
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STATUTE MILES
10 9 6 4 2 0 10 20 30 40 50

FIGURE 1.—Map of Lake Superior, showing collecting stations and localities of special interest in this study. District S-4 is a geographic area used in the analysis of commercial fishing records for State of Michigan waters of Lake Superior.

consisted of a gasoline-driven centrifugal pump (capacity, 150 gallons per minute) which was equipped with a 2-inch, high-pressure intake hose. One section of the hose extended from the lake bottom to a tightly sealed 50-gallon drum, which acted as a settling tank and in which materials pumped up were screened; a second section of hose led from the tank to the pump. A weighted funnel on the intake end of the hose was moved about over the bottom at various depths in making the collections. The lake trout fry and egg were taken from a depth of 10 fathoms. John Van Oosten (unpublished) used a similar device in 1931 in the collection of 4,410 lake trout eggs in Wisconsin waters of northern Green Bay, Lake Michigan, at depths of 15 to 25 feet. His motive power was the bilge pump of a fishing vessel; a professional diver moved the intake funnel about over the rocky bottom. Rawson and Elsey (1950) reported the recovery (by pumping) of 10 lake trout eggs from spawning grounds of Pyramid Lake, Alberta, at a depth of 10 feet.

In addition to the collection of yolk-sac fry in March 1953, 29 early fingerling lake trout, many of which still had remnants of yolk (range in length, 1.1 to 1.3 inches) were collected by trawling off the extensive Laughing Fish Point spawning grounds (Station 14, Fig. 1) on June 22–23, 1953, at depths of 12 to 16 fathoms. It seems unlikely that these fish had moved far from the hatching locality.

In view of the above observations, it appears that most lake trout in south-central Lake Superior spawn in water considerably deeper than that utilized by the species in certain other lakes. Royce (1951) observed some lake trout spawning in water less than 2 feet deep in Otsego Lake, New York, and Merriman (1935) found spawning to occur in water as shallow as 6 inches in Squam Lake, New York. The detailed descriptions of the courting and spawning behavior of lake trout given by these workers is in good agreement and is probably applicable to that of lake trout of Lake Superior.

The spawning season of lake trout in southern Lake Superior is generally in October and early November. The variation in the season in the Marquette-Munising region (statistical district S-4, Fig. 1) is indicated in Table 1, which summarizes the catch of lake trout in pounds (dressed weight) per thousand feet of large-mesh (4½ to 7 inches, extension measure) gill net, as reported by commercial fishermen to the Michigan Department of Conservation, for periods immediately preceding and following the closed seasons of 1944–1953. Commercial operators commonly fish on spawning reefs at depths of less than 20 fathoms during much of the period included in the table. Their catches thus undoubtedly reflect major changes in the numerical abundance of lake trout on the spawning grounds, despite possible distorting effects of differences in fishing time between lifts, fluctuations in the average weight of individual fish taken at different times, and probable increased activity of trout near and during the spawning period. Exceptions to this shallow-water fishing occur in the period November 10–14, when, if the first lifts reveal no concentrations of fish on the spawning grounds, nets are moved to deeper waters. In 1951, for example, the increase in catches on November 10–14 over November 5–9 presumably did not represent a resurgence of spawning activity, but a movement of the fishery to deep water, where good catches are sometimes made during this season of the year. To limit the data to the spawning-run fishery, deep-water lifts were deleted from the data when they were recognized; however, the exact fishing locality could not always be determined from the fishermen's reports.

The record of commercial catches shows that the greatest concentration of fish occurred before the closed season in 3 years (1944, 1951, and 1952) and after the closed season in 5 (1945, 1947, 1949, 1950, and 1953). In two seasons (1946 and 1948) nearly all spawning presumably occurred within the closed season prescribed by law as there was little indication of a marked concentration of fish either before or after it. For the 10-year period included in Table 1, the weight of the catch per unit of gear during the 5-day period before or after the closed season (whichever was larger) averaged 2.6 times greater (range, 1.4 in 1946 to 4.9 in 1951) than the average catch for the entire season. These values do

TABLE 1.—*Production of lake trout (pounds per thousand feet of gill net) preceding and following the closed season in the Marquette-Munising district of Lake Superior, 1944-1953*

[Number of thousands of feet of gill net are shown in parentheses. The closed season extended from October 10 to November 4.]

Year	September		October		November		Average for entire year[1]
	21-25	26-30	1-5	6-10	5-9	10-14	
1944	13.4	17.7	24.5	34.3	13.9	16.3	16.2
	(489)	(680)	(492)	(460)	(158)	(95)	....
1945	18.2	17.4	22.1	21.1	42.8	23.8	17.6
	(492)	(550)	(590)	(447)	(70)	(51)	....
1946	12.5	20.8	17.5	19.5	16.3	15.1	13.9
	(830)	(832)	(1,193)	(865)	(249)	(414)	....
1947	14.9	18.3	19.1	24.0	48.6	28.2	16.0
	(368)	(519)	(533)	(684)	(481)	(248)	....
1948	14.0	13.2	20.4	19.5	14.5	11.8	11.7
	(735)	(694)	(762)	(940)	(234)	(192)	....
1949	15.1	15.4	11.9	11.0	29.3	14.6	11.6
	(650)	(874)	(921)	(1,041)	(384)	(232)	....
1950	13.1	12.9	26.2	30.7	37.2	28.3	14.2
	(848)	(1,218)	(836)	(1,062)	(785)	(336)	....
1951	20.3	29.1	28.9	74.0	13.5	19.0	15.0
	(793)	(644)	(942)	(674)	(241)	(276)	....
1952	14.6	18.5	26.0	33.9	17.8	14.8	14.0
	(1,036)	(666)	(705)	(1,129)	(325)	(301)	....
1953	19.7	18.9	18.8	[2]....	35.0	26.0	12.1
	(968)	(714)	(946)	....	(510)	(432)	....

[1] Averages for years 1944-1949 from Hile, Eschmeyer, and Lunger (1951); data for years 1950-1953 unpublished

[2] Closed season was advanced 5 days in 1953 to begin at noon on October 5

not imply, however, that more than 2½ times as many individuals were caught during these periods, because the fish taken in large-mesh gill nets before and after the closed season often average more than double the weight of fish taken at other times during the year.[1]

In 1952 and 1953 the greatest concentration of lake trout on the spawning grounds undoubtedly occurred during the closed season, despite good commercial catches before or after. A total of 4,800 feet of large-mesh gill net lifted on spawning grounds near Marquette October 18–31, 1952, and 25,200 feet lifted October 17–23, 1953, caught lake trout at estimated rates of 157 and 65 pounds (dressed weight), respectively, per thousand feet of net, or 4.6 and 1.9 times the highest rate of capture in commercial nets lifted before (1952) or after (1953) the closed season.

Sex Ratio, Length-Frequencies, and Size at First Maturity

Among sexually mature lake trout caught in the Marquette-Munising district on or near the spawning grounds during or preceding the spawning season, males outnumbered females in collections made in 1950, 1952, and 1953 (Table 2). The percentages of males were 60.2 on September 26-October 9, 1950; 66.1 on November 8, 1950; 65.1 on October 18–31, 1952; and 69.3 on October 17–23, 1953. The percentages of males given for the 1952 and 1953 collections are minimal because the fish were not dissected and the sex was not determined for 13 taken in 1952 and for

Table 2.—*Length-frequency distribution of sexually mature lake trout collected in gill nets on or near spawning grounds in the Marquette-Munising region of Lake Superior*

Total length (inches)	Date of collection and sex									
	September 26–October 9, 1950		November 8, 1950		October 18-31, 1952[1]		October 17-23, 1953[2]		Total	
	Males	Females	Males	Females	Males	Females	Males	Females	Males	Females
22.0-23.9	..	..	..	..	..	..	2	..	2	..
24.0-25.9	6	..	2	..	6	1	7	..	21	1
26.0-27.9	15	3	6	1	20	5	26	5	67	14
28.0-29.9	26	19	18	7	22	10	37	7	103	43
30.0-31.9	18	12	26	9	12	4	40	18	96	43
32.0-33.9	6	9	11	8	8	2	25	12	50	31
34.0-35.9	5	10	6	6	3	3	12	5	26	24
36.0-37.9	3	..	5	3	..	..	2	1	10	4
38.0-39.9	1	..	..	1	..	..	..	..	1	1
40.0-41.9	..	..	..	3	..	..	..	..	..	3
Average length	29.9	31.0	30.9	32.8	29.1	29.8	30.1	31.3	30.0	31.3
Number of fish	80	53	74	38	71	25	151	48	376	164

[1] Thirteen fish of undetermined sex not included
[2] Nineteen fish of undetermined sex not included

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[1] In representative collections made in the vicinity of Marquette, 377 legal lake trout occurring in five collections taken in 4½-inch-mesh gill nets between June 2 and August 30, 1950, averaged 3.4 pounds in round weight (range of averages in the five collections, 3.1 to 3.6 pounds). A total of 208 legal fish, taken in 5½- and 6-inch-mesh gill nets in the same vicinity September 26-November 8, 1950, averaged 8.7 pounds in round weight (range of averages in the three collections, 8.2 to 9.5). In Michigan the minimum legal size is 1½ pounds.

19 in 1953. (Although most of these fish were believed to be green females, some may have been immature fish or mature males which were not yet ripe). In the combined collections, males made up 65.7 percent of the total.

Males also predominated in collections of spawning lake trout in other waters. Royce (1936) wrote that in spawn-taking operations in New York there were "about two males for each female," and the New York Conservation Department (1944) reported 77 and 78 percent males among lake trout examined during spawn-taking operations in Seneca Lake, New York, in 1941 and 1942. Miller and Kennedy (1948) found that 75 of 87 (86 percent) of the mature fish collected from a spawning run in Great Bear Lake were males. It is not known whether collections at these localities and in Lake Superior indicate a greater number of male lake trout on the spawning grounds, or whether they reflect greater activity by males than by females during the spawning season, since all fish were collected in stationary nets.

The total lengths of sexually mature male lake trout collected in large-mesh gill nets set on or near the spawning grounds in the Marquette-Munising region of Lake Superior ranged from 22.3 to 38.2 inches (average, 30.0), and lengths of females from 25.8 to 40.4 inches (average, 31.3). Although the sizes of mesh[2] used undoubtedly influenced the size of fish caught, males in all collections had a smaller average length than females, began maturing at smaller size, and were better represented among the smaller length classes than among fish of large size. For example, in the combined collections of September 26–October 9, 1950, (early in the spawning season) males composed 66 percent of the fish less than 32 inches in length and only 44 percent of the trout 32 inches long or longer; on November 8 (late in the spawning season) these percentages were 75 and 51 percent, respectively.

The available data on length of lake trout at maturity (Table 3) are not fully satisfactory since relatively few large fish were present in the collections outside the spawning season and the pre-spawning and spawning-run collections may have been biased toward overrepresentation of mature individuals[3]. Scanty and defective as the records may be, they give strong evidence that lake trout of both sexes first reach maturity at a relatively great size and that males become mature at a smaller length than do females. The shortest mature male in the non-spawning samples was 25 inches (lower limit of 1-inch interval), but the spawning collections included mature males as short as 22 inches. No mature females less than 25 inches long were in either group. The largest immature males were in the 29-inch class in both non-spawning and spawning samples, as was the largest immature female of the non-spawning collections. The spawning-run samples, however, included 5 larger immature females, 4 in the 30-

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[2] The sizes of mesh in inches (extension measure) of gill nets used in the collections were as follows: September 26-October 9 and November 8, 1950—5½ and 6; October 18-31, 1952, 5½; and October 17-23, 1953—4½, 5, 5½, and 6.

[3] Data were restricted to collections in which the sex of all fish caught was determined by dissection, at a season when evaluation of maturity of the gonads was presumed to be unquestionable.

TABLE 3.—*Length-frequency distribution, sex, and maturity of lake trout collected in southern Lake Superior, July 25–December 21, 1950*

Total length (inches)	Non-spawning[1]						Spawning[2]					
	Males			Females			Males			Females		
	Immature	Mature	Percent-age mature	Immature	Mature	Percent-age mature	Immature	Mature	Percent-age mature	Immature	Mature	Percent-age mature
<22.0	157	..	0	134	..	0	121	..	0	82	..	0
22.0-22.9	19	..	0	28	..	0	5	2	29	7	..	0
23.0-23.9	14	..	0	17	..	0	5	1	17	3	..	0
24.0-24.9	6	..	0	6	..	0	2	9	82	3	..	0
25.0-25.9	6	1	14	4	1	20	1	11	92	4	3	43
26.0-26.9	2	2	50	4	1	20	..	17	100	6	5	45
27.0-27.9	1	..	0	1	1	50	1	24	96	7	10	59
28.0-28.9	1	1	50	..	..	..	..	32	100	5	27	84
29.0-29.9	2	..	0	1	1	50	1	26	96	4	18	82
30.0-30.9	..	1	100	..	1	100	..	29	100	4	27	87
31.0-31.9	..	..	..	..	..	..	..	30	100	1	11	83
>31.9	..	..	..	..	1	100	..	44	100	..	56	100
Total	208	5	2	195	6	3	136	225	62	126	157	55

[1] Collected July 25, August 11, 17, 30, November 22, December 12, 14, 21 in 4½-inch-mesh (extension measure) gill nets off Keweenaw Point, Marquette, and Munising

[2] Collected September 8, 9, 12, 16, 20, 26, 29, October 9, November 8 in 4½-, 5½-, and 6-inch-mesh gill nets off Ontonagon, Keweenaw Point, Marquette, and Munising

inch and 1 in the 31-inch interval. If the mean between the smallest mature and the largest immature fish is accepted as a rough estimate of average size at first maturity, the following figures are obtained: males, 25½ inches; females, 28 inches.

The possibility remains that some of the larger immature fish may have spawned earlier in life, even though their reproductive organs did not mature during the year of collection. The numbers of immature fish tended to diminish progressively with increasing size, however, and no immature fish were found among 57 females and 44 males with total lengths of 32 inches or more. No gonads were seen which conformed to Kennedy's (1954) description of the gonads of mature non-spawning lake trout collected in Great Slave Lake. Such "infecund" fish of large size were also observed among lake trout in certain other waters (Fry and Kennedy, 1937; Fry, 1949; Miller and Kennedy, 1948).

The observations on size at sexual maturity of lake trout in Lake Superior conform closely to the findings of Dymond (1928), who reported that female lake trout in the western end of Lake Ontario do not begin to spawn until they reach a weight of approximately 6 pounds (equivalent to a length of about 26½ inches in Lake Superior fish), and of Royce (1951) who wrote that lake trout in Seneca Lake, New York, do not mature until they are 26 to 30 inches in total length. In contrast, lake trout in a number of Canadian waters may become mature at lengths ranging between 14 and 18 inches (Fry, 1939; Miller and Kennedy, 1948; Kennedy, 1954). Sexual maturity at lengths of 15 to 16 inches was also reported in Skaneateles Lake, New York (Royce, 1951, referring to unpublished data of H. J. Rayner), and some siscowets collected in Lake Superior, about 45 miles north of Grand Marais, Michigan, were mature at similar lengths (p. 69).

MOVEMENT ON THE SPAWNING GROUNDS AND HOMING BEHAVIOR

Some male lake trout apparently remain on or near the spawning grounds several weeks during the spawning season. This behavior was indicated by recoveries of marked fish in the commercial fishery following the tagging of 187 large lake trout (average total length, 30.1 inches; range, 22.3–36.5) during the period October 17–23, 1953, on spawning grounds near Marquette (Stations 5, 7, 10, and 14, Fig. 1). Of this group, 132 were males and 36 were females; the sex of 19 was not determined. Later recoveries, 18 to 26 days after marking, included 9 males and 1 fish of unknown sex, all caught within 8 miles of the place of release, on the same or a contiguous spawning area. Three males and 1 fish of unknown sex were recovered during the same period at distances of 26 to 97 miles, but in shallow water at localities recognized by commercial fishermen as lake trout spawning grounds. These fish apparently had moved to other breeding areas during the spawning season. One male was caught 34 days after tagging, in deep water (60 fathoms), 37 miles from the place of release.

Although some fish apparently remained near the spawning grounds during other seasons of the year (1 recovery in April, 1 in May, and 1 in July 1954, all within 5 miles of the locality of release), others dispersed widely. Eight recaptures during the period December 10, 1953-September 9, 1954, were at distances of 14 to 189 miles (average, 54) from the place of release.

Later recoveries, as fish again started to move toward their spawning grounds, corroborated strongly the conjecture of Eschmeyer, Daly, and Erkkila (1953) that, although large lake trout in Lake Superior dispersed widely through the lake after spawning, some (perhaps many or most) returned to their established spawning grounds during subsequent spawning seasons. Twelve of 14 recoveries made between September 23 and November 12, 1954, from the lake trout tagged on the spawning grounds near Marquette in October 1953 were within 8 miles of the place of release, at depths of less than 25 fathoms. One fish was caught on different spawning grounds 28 miles away, and another, which had probably finished spawning, was taken at 65 fathoms, 34 miles from the tagging locality.

Additional evidence on the movement of lake trout following spawning resulted from the tagging of 96 large fish (average total length, 29.5 inches; range, 24.3 to 35.8) on spawning grounds near Marquette (Station 10, Fig. 1), October 18–31, 1952. After 10 recoveries between November 13, 1952, and September 11, 1953, at distances ranging from 13 to 198 miles (average, 71), 12 lake trout were recaptured near or during the subsequent spawning season, September 14-November 10, 1953, within 8 miles of the tagging locality. During this same period, however, 5 fish were captured on other spawning reefs 18 to 62 miles away. Six later recoveries, April 6-July 7, 1954, were 23 to 120 miles (average, 78) from the tagging locality, although 5 fish caught between August 9 and September 9, 1954, were within 5 miles of the place of release. One tagged trout was recaptured on October 2, 1954, on a reef 27 miles from the tagging locality and 3 of 4 recoveries on November 5–9, immediately following the closed season, were within 8 miles of the place of release; the other was on a reef 21 miles away.

Eschmeyer, Daly, and Erkkila (1953) listed 7 recoveries during the period September 10-October 9, 1952, from 116 large lake trout tagged off Keweenaw Point (Station 4, Fig. 1) on October 11–27, 1950. Six of these recaptures were within a radius of about 20 miles from the tagging locality and 1 was 140 miles away. Two recoveries from this group of fish, on September 14, 1953, and September 30, 1954, were within 8 miles of the tagging locality. One fish was caught on other spawning grounds (November 6, 1953), 55 miles from the place of release.

A precise conclusion as to the homing tendencies of spawning lake trout is made difficult by the fact that a fish captured and tagged or recaptured in a particular spawning area may not in fact be on its "home" ground, but rather may be enroute to or from it. Although all spawning lake trout possibly may exhibit homing behavior, available evidence permits only the statement that the tagged individuals showed a proclivity to return during later years to spawning grounds on which they had been marked, even though many of them ranged long distances between spawning seasons. The recoveries from the two experiments (1952 and 1953) in the Marquette area indicate that 27 of 36 (75 percent) tagged fish recovered near or during spawning seasons subsequent to that of tagging were caught on the spawning grounds on which they were released.

DEVELOPMENT OF THE GONADS

The ovaries of lake trout—paired, elongated organs suspended near the dorsal side of the body cavity, beneath the air bladder—conform in most details to the description of ovaries of salmonoid fishes given by Kendall (1921).

The left ovary was usually the heavier in mature fish collected in southern Lake Superior August 11-November 8, 1950, and August 27-October 10, 1951. In 64 lake trout whose left and right ovaries were weighed separately, the left was heavier in 72 percent, lighter in 16 percent, and in 12 percent the two ovaries were of about equal weight (difference less than 5 percent). For all fish the weight of the right ovary averaged 86 percent of the weight of the left. The size of eggs was the same in ovaries of unequal weight but the numbers differed according to the difference in weight. The heavier ovary had the larger number of eggs in all 28 of the fish for which estimates or counts of egg numbers were made separately for each ovary and in which ovary weights differed by as much as 5 percent.

Differences between the size of right and left male gonads were sometimes apparent upon dissection, although few were weighed separately. Of 5 mature males collected on October 18, 1952, the testes were of about equal weight (difference less than 5 percent) in 2 fish; in the other 3 the weights of the right testes equalled 9, 74, and 83 percent of the weights of the larger left testes. The first of the three values is extreme, and may have been the result of partial atrophy or disease of the one organ.

The weights of male and female gonads, expressed as percentage of the total weight of lake trout, preceding, during, and following the spawning season of 1950, are shown in Table 4. Average diameters (determined by use of an egg-measuring trough) of the eggs in samples of 50, taken at random from the ovaries of sexually mature females, are also shown.

Most gonads were preserved in 10-percent formalin. They were weighed after removal of excess liquid from the surface by blotting. The effect of preservation on the estimation of weight was determined by comparisons of weights of gonads in both the fresh and preserved condition for 14 mature males, 3 immature females, and 6 maturing females. These comparisons indicated the following factors for conversion from preserved to fresh weights: mature males, 1.176; immature females, 1.073 (value used also for spent females and immature males); and ripening females, 1.034. Although these conversion factors are based on limited data, they are

TABLE 4.—*Percentage of total weight composed by gonads of lake trout in southern Lake Superior, 1950*

[Numbers of fish in parentheses]

Sex, maturity, and date of collection	Total length (inches)								Average diameter of eggs (millimeters)
	12.0-15.9	16.0-19.9	20.0-23.9	24.0-27.9	28.0-31.9	32.0-35.9	36.0-39.9	Average	
Immature females									
September 8—November 22	0.1 (11)	0.1 (19)	0.2 (21)	0.5 (12)	0.6 (5)	...	...	0.2 (68)	...
Mature females									
August 11-30	...	...	...	5.6 (1)	4.7 (2)	...	...	5.0 (3)	3.7 (3)
September 8-9	...	...	...	7.2 (4)	6.8 (13)	8.5 (3)	...	7.1 (20)	4.2 (20)
September 16-29	...	...	...	9.3 (8)	9.6 (18)	11.8 (7)	...	10.0 (33)	4.7 (33)
October 6-9	...	...	...	11.2 (2)	11.8 (16)	13.3 (9)	...	12.3 (27)	4.9 (27)
November 8	...	...	...	12.9 (1)	11.7 (1)	...	...	12.3 (2)	5.1 (25)
November 8[1]	...	...	...	...	1.7 (11)	1.9 (12)	...	1.8 (23)	1.3 (23)
Immature males									
September 8-20	0.1 (9)	0.1 (13)	0.1 (19)	0.1 (1)	0.1 (1)	...	...	0.1 (43)	...
Mature males									
September 8-9	...	...	3.2 (1)	2.7 (7)	2.4 (18)	4.5 (1)	...	2.6 (27)	...
September 16	...	...	2.6 (3)	2.9 (18)	3.7 (2)	4.8 (2)	3.9 (1)	3.1 (26)	...
November 8	...	...	...	2.0 (4)	1.5 (19)	1.9 (11)	2.9 (1)	1.7 (35)	...

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[1] Ripe or nearly spent ovaries from which residual mature eggs were removed before weighing. The average egg diameter is for the larger of two size groups of immature eggs remaining in the ovaries

believed to represent an improvement over unconverted preserved weights.

The weight of the ovaries equalled only 0.1 percent of the total weight of immature females less than 20 inches long. For fish of larger size this percentage increased progressively from 0.2 percent in fish 20.0 to 23.9 inches long to 0.6 percent for fish in the 28.0- to 31.9-inch group. Immature males did not show this increase. The testes made up 0.1 percent of the total weight in each of the five length groups over the range of 12.0–31.9 inches.

The ovaries of mature females composed a progressively greater percentage of the body weight as the spawning season approached. The average percentages were: 5.0 on August 11–30; 7.1 on September 8–9; 10.0 on September 16–29; and 12.3 for fish collected near the time of spawning (October 6–9 and November 8 collections combined). For ripe or nearly spent fish collected on November 8, the weight of the ovary, after removal of all remaining mature eggs, was equal to 1.8 percent of the total weight of the fish.

A trend toward an increase in the percentage of total weight composed by the reproductive organs with an increase in the size of fish was demonstrated by data for the two largest collections of females with maturing ovaries. For collections of September 16–29, this percentage increased from 9.3 percent for fish in the 24.0- to 27.9-inch group to 11.8 percent for fish in the 32.0- to 35.9-inch class. In the October 6–9 collections values for these same groups were 11.2 and 13.3 percent, respectively. As might be expected, this increase was associated with an increase in egg production per pound of fish among larger individuals (Table 8). A progressive increase in the average diameter of the eggs, from 3.7 millimeters (range, 3.2–4.1) in fish taken August 11–30 to 5.1 millimeters (range, 4.6–5.7) in fish collected on November 8, was associated with the increase in weight of the ovaries with the progress of the season. (No correlation was observed between the diameter of the eggs and the size of the fish within the range of lengths of fish examined.) The larger immature eggs remaining in ovaries of ripe or nearly spent lake trout collected on November 8 had an average diameter of 1.3 millimeters.

The weights of the gonads of mature males collected September 8–9, 1950, averaged 2.6 percent of the total weight of the fish. On September 16 this percentage was 3.1. By November 8, late in the spawning season, depletion of the gonads had progressed to the stage where their weight averaged only 1.7 percent of the total weight.

The proportion of the total weight made up by gonads of lake trout collected in the Marquette-Munising district of Lake Superior in 1951–1953 (Table 5) shows the same progressive increase with progress of the season demonstrated by the 1950 data of Table 4. The average proportion of the total weight composed by the ovaries and the average diameter of the eggs of 2 large females examined on May 16, 1951, were about the same as for spent females collected November 8, 1950, and for spent fish collected October 19–23, 1953. This agreement suggests that the increase in weight of the ovaries accompanying development of eggs for fall

TABLE 5.—*Percentage of total weight composed by gonads of mature lake trout in southern Lake Superior, 1951-1953*

[Numbers of fish in parentheses]

Sex and date of collection	Total length (inches)						Average diameter of eggs (millimeters)
	20.0-23.9	24.0-27.9	28.0-31.9	32.0-35.9	36.0-41.0	Average	
Females							
May 16, 1951	...	...	...	...	1.6 (2)	1.6 (2)	1.6 (2)
July 22, 1953	...	2.7 (2)	...	6.0 (1)	...	3.8 (3)	3.3 (3)
August 20-27, 1951	...	7.8 (3)	8.5 (6)	6.9 (1)	...	8.1 (10)	4.4 (10)
October 8-10, 1951	...	10.2 (1)	16.9 (6)	15.7 (6)	16.8 (2)	16.0 (15)	5.2 (15)
October 17-20, 1953	...	17.3 (1)	...	17.7 (3)	22.0 (1)	18.5 (5)	5.4 (1)
October 19-23, 1953[1]	...	...	1.7 (5)	1.9 (1)	...	1.7 (6)	...
Males							
May 16, 1951	...	...	...	...	0.7 (2)	0.7 (2)	...
June 17, 1953	...	1.5 (2)	...	...	...	1.5 (2)	...
July 22, 1953	1.2 (1)	0.8 (1)	0.9 (2)	...	...	1.0 (4)	...
September 29, 1953	2.3 (1)	...	...	...	...	2.3 (1)	...
October 18, 1952	...	2.1 (1)	2.5 (4)	...	...	2.4 (5)	...
October 17 23, 1953	2.1 (1)	2.2 (2)	3.1 (13)	3.7 (4)	...	3.1 (20)	...

[1] Spent or ripe ovaries from which residual mature eggs were removed before weighing

spawning had not yet begun. This increase was well underway in 3 fish collected July 22, 1953, whose gonads averaged 3.8 percent of the total weight (average egg diameter, 3.3 millimeters). On August 20–27, 1951, the percentage was 8.1 (egg diameter, 4.4 millimeters). The relative weight had nearly doubled, to 16.0 percent (egg diameter, 5.2 millimeters) by October 8–10 of that year; and for 5 fish collected October 17–20, 1953, the percentage was 18.5. Thus the limited number of ovaries of maturing females collected in 1951 and 1953 made up a somewhat higher percentage of the weight of the fish than they did in lake trout taken on comparable dates in 1950 (Table 4). The range of variation was wide, however, and a larger series of specimens would be required to detect significant annual differences, or to corroborate for southern Lake Superior Fry's (1949) observation in Lake Opeongo, Ontario, that average egg production (presumably closely related to weight of the ovary) of lake trout of all ages may be consistently above or below average during some years.

Few testes were weighed during 1951–1953, but the limited data suggest an irregular increase in weight during the season, from 0.7 percent of the total weight in 2 large males collected on May 16, 1951, to 3.1 percent for fish collected October 17–23, 1953. In all samples (1950–1953) the weight of the testes of mature males exceeded 5 percent of the total weight in only 1 fish (collected September 16, 1950).

For both males and females in the several collections the proportional weight of the gonads of immature fish (collected September 8-November 22, 1950) was smaller than that of spent mature fish. For individual mature fish the minima observed were 0.7 percent for males and 1.1 percent for females; for immature fish of the 1950 collections the maximum weights of the gonads equalled 0.2 percent for males and 0.8 percent for females.

RELATIONSHIP OF CONDITION TO SPAWNING

The coefficient of condition *C* [4] (Table 6) for three 4-inch length groups of mature lake trout collected in 1950 indicates that within the length range of 24.0–35.9 inches condition did not change consistently with length and that the average values for all fish (right-hand column) were in reasonably good agreement with those for fish of each 4-inch length class. A progressive increase in the condition of females with the approach of the spawning season was not indicated, despite the progressive increase already mentioned in the proportion of the total weight composed by the ovaries. In collections represented by 20 or more fish *C* was 34.4 on September 8–9, 35.1 on September 16–29, and 33.8 on October 6–9.[5] This value diminished to 29.3 as an average for 23 spawning fish (9 to 3,750 mature eggs in their ovaries) collected on November 8. When the weight of the residual eggs was deducted from the weight of each fish and the *C* value recomputed, this average (applying then to fully spent females) was 28.9.

The failure of female lake trout to improve in condition although an increasing percentage of the total weight was being contributed by the gonads is clearly indicative of a decrease in body condition (when considered exclusive of gonads). The nature of this decrease is shown more clearly when the condition factor is computed after the weight of the gonads has been deducted from the total weight of the fish (here termed the "basic" condition factor). The resulting values declined progressively

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[4] $C = \frac{W\, 10^5}{L^3}$ where W = weight in pounds and L = total length in inches.

[5] Two other fall-spawning Great Lakes species exhibited a decline in the condition of mature fish prior to the spawning season, the kiyi of Lake Michigan (Deason and Hile, 1947) and the whitefish of Lake Erie (Van Oosten and Hile, 1949).

TABLE 6.—*Condition factors* (C) *of lake trout collected in southern Lake Superior, 1950*
[Numbers of fish in parentheses]

Sex and date of collection	Type of condition factor[1]	Total length (inches)			
		24.0-27.9	28.0-31.9	32.0-35.9	Average
Females					
August 11-30	*C*	33.1	33.2	....	33.2
	Basic *C*	31.2	31.7	....	31.5
		(1)	(2)		(3)
September 8-9	*C*	33.3	34.0	37.3	34.4
	Basic *C*	30.9	31.7	34.2	31.9
		(4)	(13)	(3)	(20)
September 16-29	*C*	35.8	34.3	36.5	35.1
	Basic *C*	32.5	31.1	32.2	31.7
		(8)	(18)	(7)	(33)
October 6-9	*C*	34.4	33.7	33.8	33.8
	Basic *C*	30.5	29.8	29.3	29.7
		(2)	(16)	(9)	(27)
November 8	*C*	35.6	31.3	....	33.4
	Basic *C*	31.0	27.7	....	29.4
		(1)	(1)		(2)
November 8[2]	*C*	....	29.4	28.5	28.9
	Basic *C*	....	28.9	27.9	28.4
			(11)	(12)	(23)
Males					
September 8-9	*C*	32.6	33.5	39.6	33.5
	Basic *C*	31.7	32.7	37.8	32.6
		(7)	(18)	(1)	(26)
September 16	*C*	33.8	33.0	36.2	33.9
	Basic *C*	32.8	31.7	34.4	32.8
		(18)	(2)	(2)	(22)
October 6-9[3]	*C*	30.6	31.2	35.0	31.1
		(9)	(21)	(1)	(31)
November 8	*C*	28.2	32.0	30.5	31.0
	Basic *C*	27.6	31.5	29.9	30.5
		(4)	(19)	(11)	(34)

[1] Basic *C* refers to the condition factor computed after deduction of the weight of the gonads from the weight of the fish

[2] Spent or ripe fish from which weight of residual mature eggs was deducted before computation of *C*

[3] The testes of fish of this collection were not weighed

for fish in collections made between September 8–9 and November 8. The greatest rate of decline was between the September 16–29 and October 6–9 collections, when the average coefficient diminished from 31.7 to 29.7; it declined further to 28.4 for ripe and spent fish collected November 8.

The decline in basic condition with the increase in percentage of total weight composed by the gonads can also be demonstrated in the collection of October 6–9, considered alone. In fish of this collection, the basic condition factor and the percentage of the body weight composed by gonads showed a negative correlation ($r = -0.397$; $p < 0.05$) [6].

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[6] Length of fish and basic condition showed no correlation.

Basic condition factors of maturing females collected in other years were in close agreement with those of fish caught on comparable dates in 1950. Females collected August 20–27, 1951, had an average basic condition factor of 31.6; the factor on October 8–10 was 29.8 (comparable 1950 values were 31.6 and 29.6). Five nearly ripe females captured October 17–20, 1953, had an average basic factor of 29.6.

Among mature males collected in 1950, changes in condition related to spawning were not usually as great as for females collected during the same year, although they reflected the same drop in condition shown by the females between the September and October collections. The condition factors (whole fish) of males averaged 33.7 on September 8–16 and 31.1 on October 6–9. Basic condition was 32.7 for the September 8–16 fish and 30.5 for fish collected November 8. Basic factors are not available for collections between these dates during 1950, but the factors for males collected October 18, 1952, and October 17–23, 1953, had the intermediate values of 31.8 and 32.2, respectively.

Although whole-fish condition factors of males were lower than those of females taken at comparable dates during the period September 8-October 9, the condition of males was better than that of spawning and spent females on November 8, toward the end of the spawning season. The basic condition factor of males was higher than that of females in all comparable collections.

The loss of condition prior to spawning may have been related in part to a reduction in the amount of food eaten as the spawning season neared. Although Martin (1949) noted that lake trout fed throughout the spawning period, Miller and Kennedy (1948) found that 69 percent of the stomachs of 87 mature lake trout caught early in the spawning season in Great Bear Lake were empty; stomachs of the others were nearly empty. Observations in southern Lake Superior indicated that feeding was markedly reduced near the time of spawning. Of 85 mature fish whose stomachs were examined on November 8, 1950, when nearly all fish were ripe, 76 (89 percent) were empty (stomachs of each of 3 immature fish taken in the same nets contained food). Of 32 fish (4 green, 28 ripe) examined October 17–23, 1953, 31 (97 percent) contained no food. This situation is in contrast to collections on September 8, 1950, when stomachs of only 10 of 43 mature fish (23 percent) were empty, and on September 16, 1950, when 28 of 52 (54 percent) contained no food. (Fishing time of the nets presumably tended to minimize rather than to increase this seasonal difference, since nets lifted in September had been out 4 to 7 nights, whereas nets lifted in November 1950 and October 1953 had been out for shorter periods). It is not known whether the difference in percentage of empty stomachs on September 8 and on September 16 are indicative of a progressive decline in feeding activity (no information for intermediate collections). However, the data strongly suggest that feeding had diminished pronouncedly by the time of spawning.[7]

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[7] Limited data available indicated that the physical absence or presence of food in stomachs at the time of collection did not in itself materially affect the estimate of average basic condition.

FECUNDITY

Of 79 lake trout ovaries for which egg counts or estimates were made, 59 were collected in the Marquette-Munising district of Lake Superior, 13 west of Ontonagon, Michigan (Station 1, Fig. 1), and 7 near Keweenaw Point (Station 4). The fish were caught in large-mesh commercial or experimental gill nets (73), or pound nets (6). Of the total, 69 were taken August 18-November 8, 1950, 9 were collected August 27-October 10, 1951, and 1 on October 18, 1953.

Methods of estimating egg numbers.—One volumetric and two gravimetric methods for estimating numbers of eggs in ovaries were evaluated. In all three methods, eggs in measured samples of the ovary were counted and the numbers of eggs in the remainder estimated by direct proportion. Accuracy of estimates was determined by complete counts.

In the volumetric method the eggs in a sample and the eggs in the remainder of the ovary were measured by water displacement in a graduated cylinder. In the first of the gravimetric methods, excess liquid was blotted from the surface of the ovary and the eggs in a sample and the eggs in the remainder of the ovary were weighed on a triple-beam balance (graduated to 0.1 gram). For both the volumetric and the wet-weight methods as many as six samples on which estimates were based were taken from the ovaries of a single fish, from various loci (*e. g.*, anterior, middle, and posterior portions of the left and the right ovary). Estimates used in the tests were restricted to the ovary from which the sample was taken, although the size of the nearly mature eggs did not differ significantly between ovaries of the same fish or between various parts of the same ovary.

In the second or dry-weight gravimetric method the preserved ovaries were broken into sections and the eggs separated from much of the ovarian tissue by rubbing between the hands. The eggs were then placed in shallow pans or in bags of loosely woven cloth and put on the shelves of a drying oven, where they were left (with oven ventilators open) at a temperature of about 80° to 90° C. for 2 to 6 hours. During this period the eggs were stirred or turned occasionally to facilitate uniform drying. After the drying, random samples of eggs and the remainder of the eggs in the lot were weighed on an analytical balance. Estimates were made only for the eggs of an ovary or ovaries dried in a single pan or bag, because drying was seldom exactly uniform among the eggs in different containers, even though they were from the same fish. In testing the method, five samples of 100 dried eggs each were weighed from an ovary or ovaries of each of 17 fish.

The volumetric method was poorer than either of the gravimetric methods for estimating numbers of eggs in lake trout ovaries (Table 7). The percentage error of the estimates covered a wider range and the mean deviation (average of absolute values of percentage error) was greater (3.2 percent) in the volumetric than in the gravimetric methods. Only 17 percent of the samples gave estimates with an error of less than 1 percent.

In the wet-weight method of estimation the range in percentage error of estimates was less and the mean percentage deviation was markedly lower (1.9) than in the volumetric method. Forty-five percent of the samples gave an error of estimate of less than 1 percent.

Estimates by the dry-weight method had the smallest range in error and had the smallest mean deviation (0.7 percent) of the three methods tested. For 85 100-egg samples the percentage error of estimate ranged from −4.7 to 3.2 (average, −0.3) and the mean deviation was 0.7 percent; 51 percent of the samples gave an error of estimate of less than 1 percent. This greater accuracy was obtained even though the 100-egg samples composed an average of only 4.3 percent of the total number of eggs in the ovaries, as compared to 15.0 and 15.1 percent in the tests of the volumetric and wet-weight methods. When five 100-egg samples were combined as a single estimate for each of the 17 fish, the range of the percentage error was further reduced (−2.2 to 1.2) and 65 percent of the samples had an error of less than 1 percent. Average percentage error of estimate and percentage mean deviation were of course the same as for the 100-egg samples because both values were averages of identical data.

TABLE 7.—*Comparison of three methods of estimating numbers of eggs in lake trout ovaries*

Number of samples	Percentage of total eggs in sample		Percentage error of estimates		Mean percentage deviation[1]	Percentage of estimates with less than 1.0 percent error
	Range	Average	Range	Average		
Volume						
24	8.0–24.9	15.0	−6.0 to 8.5	1.7	3.2	17
Wet weight						
29	8.0–24.9	15.1	−5.1 to 4.6	−0.7	1.9	45
Dry weight						
85[2]	1.0– 7.7	4.3	−4.7 to 3.2	−0.3	0.7	51
17[3]	4.9–38.5	21.3	−2.2 to 1.2	−0.3	0.7	65

[1] Average of absolute values
[2] Samples of 100 eggs
[3] Samples of 500 eggs

Although the dry-weight method is technically more accurate,[8] the estimation of numbers of eggs in lake trout ovaries can be accomplished more easily by the wet-weight method. Eggs need not be removed from the ovary (except in the sample which is counted), the drying process is eliminated, and weighing proceeds more rapidly on a triple-beam than on an analytical balance. In view of the wide variation in numbers of eggs produced by lake trout of similar length or weight, the errors of estimate can be considered unimportant in any practical study of lake trout fecundity.

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[8] In the present study all values for egg production are based either on dry-weight estimates (500-egg samples) or on complete counts.

Still another method of estimating the fecundity of lake trout was employed by Fry (1949) who measured the diameters of 10 maturing eggs and weighed the ovaries; estimates were then made by reference to a conversion diagram showing diameter of maturing eggs plotted against number of eggs per gram of ovary.

Numbers of eggs produced.—In 70 lake trout from southern Lake Superior with total lengths of 25.1 to 38.0 inches and weights of 5.8 to 19.6 pounds, the egg production per fish ranged from 2,476 to 17,119 (Table 8; Figs. 2 and 3). The average number of eggs ranged irregularly upward from 3,383 for fish in the 25.0- to 26.9-inch length class to 13,836 in fish in the 37.0- to 38.9-inch class. However, the individual variability was so great that the maximum number of eggs produced by a fish in the 25.0- to 26.9-inch group (5,645) was greater than the minimum number produced by a fish of the 31.0- to 32.9-inch class (5,414). The widest range in egg production within any 1-inch or 1-pound interval was between two lake trout, each 33.6 inches long, with weights of 13.1 and 13.2 pounds, and with egg counts of 5,791 and 14,260 (the latter about 2.5 times larger than the former). In each of six 2-inch length classes represented by 6 or more individuals, the maximum egg number was about double that of the minimum count or estimate for a fish of the same length group. This wide range in egg production is not regarded as indicative of, or associated with, racial differences. Fish caught in the same nets at the same time at each of the several localities of collection showed wide variation in egg numbers; nor did commercial fishermen recognize distinct races among the fish used in the fecundity study.

TABLE 8.—*Production of eggs by lake trout in southern Lake Superior*

Total length (inches)		Average weight (pounds)	Number of fish	Number of eggs per fish		Number of eggs per pound of fish	
Interval	Average			Range	Average	Range	Average[1]
25.0-26.9.......	26.0	6.2	9	2,476- 5,645	3,383	400- 844	546
27.0-28.9.......	28.0	7.4	15	3,017- 6,528	4,253	424- 908	573
29.0-30.9.......	30.1	9.4	13	3,622- 7,170	4,995	397- 819	532
31.0-32.9.......	32.2	11.6	17	5,414-12,700	8,667	485-1,093	743
33.0-34.9.......	33.6	13.9	8	5,791-14,260	8,881	441-1,084	645
35.0-36.9.......	35.6	16.5	6	9,062-17,119	11,603	490- 873	705
37.0-38.9.......	37.6	19.3	2	12,906-14,766	13,836	673- 757	715
39.0-40.9.......	40.2	....[2]	2	10,877-12,701	11,789	....	...

[1] Mean of figures determined for individual fish

[2] These fish were not weighed. Seven unweighed fish of other length classes were not included in this table, but their egg production is plotted in Figure 2

Change in average egg production per pound of fish with increasing size was irregularly upward. A sharp change of level took place between the 29.0- to 30.9-inch and the 31.0- to 31.9-inch intervals when the number of eggs per pound increased from 532 to 743. In the three length classes below 31.0 inches the eggs per pound ranged from 532 to 573; at lengths of 31.0 inches and greater the averages ran from 645 to 743. Grand average values for the two larger length intervals were: 25.0–30.9 inches, 552 eggs per pound; 31.0–39.9 inches, 711 eggs per pound. Because of this change in egg production with increase in length of the fish, no single figure is accurately descriptive of Lake Superior lake trout. The grand average number of eggs per pound of fish for the lake trout on which the data of Table 8 were based was 646.

In the graphical presentation of data on egg production of lake trout in southern Lake Superior (Figs. 2 and 3) the triangular points represent siscowets, which are discussed separately in the next section. The curves (fitted by inspection) are based only on data for lake trout.

Despite the wide variation in fecundity among individual fish, a line drawn by inspection through the plotted points relating egg production to length (Fig. 2) assumes a sigmoid form. The curve is flattest between the length of 25.0 and 28.0 inches, where it shows an average increase of about 430 eggs per inch increase of length. From this level the curve rises rather abruptly, reaching its greatest slope (about 1,100 eggs per inch of length) between 30 and 33 inches. This steep section reflects the marked increase in egg production of fish of the 31.0- to 32.9-inch length class already noted in Table 8. Beyond 35 inches the slope of the curve decreases gradually; the scattered data for lengths over 36 inches suggest an average increase of about 700 eggs per inch of length.

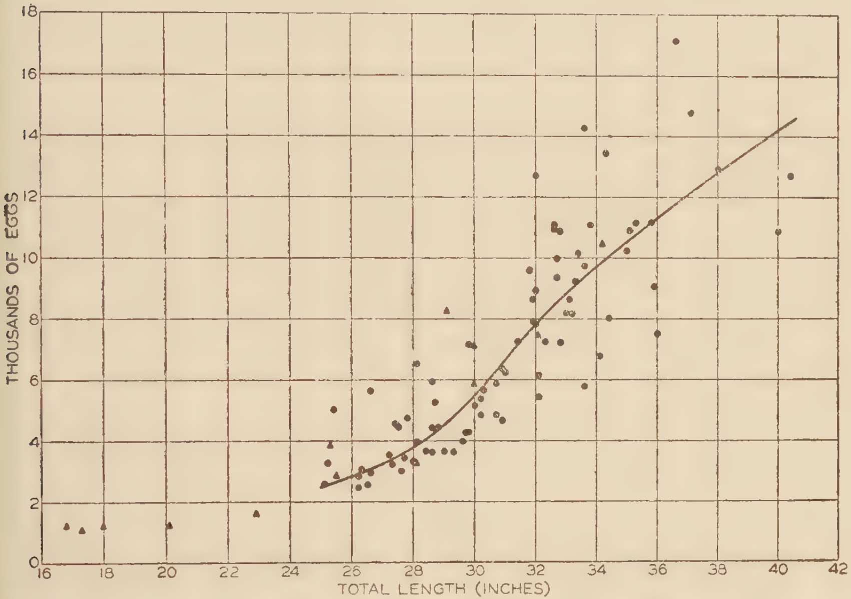

FIGURE 2.—Relationship of length of fish to number of eggs in ovaries of lake trout. Solid dots (on which the curve is based) represent individual lake trout; triangular points are siscowets. The data are summarized in Tables 8 and 9.

Although the curve of the relationship of egg production to weight (Fig. 3) gives some indication of a sigmoid form, especially between the weights of 6 and 16 pounds, the straight line seems to give a reasonably adequate fit to the scattered points. This line, drawn by inspection, extends from a production of about 2,900 eggs at a weight of 6 pounds to 14,600 eggs at 20 pounds, and thus has a slope depicting an increase of about 836 eggs per pound increase of fish weight between these extremes.

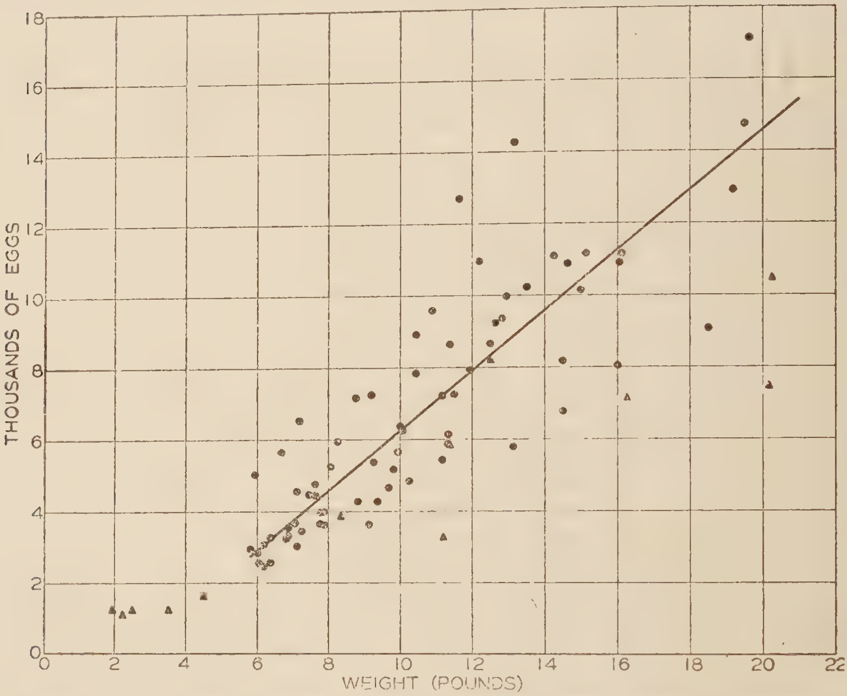

FIGURE 3.—Relationship of weight of fish to number of eggs in ovaries of lake trout. Solid dots (on which the curve is based) represent individual lake trout; triangular points are siscowets. The data are summarized in Tables 8 and 9.

In his study of fecundity of Lake Ontario lake trout, Dymond (1928) found from 2,542 to 18,051 eggs in the ovaries of 25 lake trout (range in fork length, 24 to 35¼ inches) collected August 4–23, 1927, off Port Credit, Ontario. The average production was 721 eggs per pound of fish. Two fish of similar length and weight (26¼ and 27½ inches; 9 pounds, 2 ounces, and 9 pounds, 1 ounce) produced 3,340 and 11,931 eggs, respectively, indicating a wide variation similar to that found in lake trout from Lake Superior. Milner (1874) reported that a 24-pound lake trout from Lake Michigan contained 14,943 eggs. Edward Schneberger (unpublished) determined fecundity of 16 ripe Lake Michigan lake trout in

1936. These fish were from 24¼ to 36 inches long and weighed 4 to 15½ pounds. Egg production ranged from 2,970 to 14,648 eggs per fish, or from 478 to 1,237 per pound of fish (grand average, 776). Fry (1949) reported egg counts for lake trout of Lake Opeongo, Ontario, to range from a mean of 1,200 for age-group V to 15,000 for age-group XVII. Average fork lengths of fish at these ages were 14.6 and 31.4 inches, respectively.

REPRODUCTION OF SISCOWETS

The egg production was determined for 13 siscowets 16.8 to 34.2 inches long, collected at scattered localities in Lake Superior in 1950, 1953, and 1954 (Table 9; triangular points in Figs. 2 and 3). Identity of the specimens is not based on taxonomic characters but on identification by commercial fishermen, who usually separate lake trout ("leans") and siscowets ("fats", and presumed intergrades or smaller fats known as "half-breeds") before marketing the fish. This identification, based largely on quantity of fat lining the body cavity and on gross appearance, seems to be uniform among fishermen of different localities.[9] Usually the condition factor of fish identified as siscowets is higher (often markedly so) than for lake trout of the same length (*cf.* right-hand column of Table 9 with corresponding data of Table 6). However, this criterion is invalidated by an overlap in coefficient of condition which occurs toward the extremes of the range for each subspecies.

Of the fish for which data are given in Table 9, the 5 smallest were considered half-breeds and the remainder were regarded as fats. They were caught at depths of 50 to 80 fathoms with the single exception of a 22.9-inch fish (No. 5) collected between 10 and 20 fathoms on September 16, 1950. Although siscowets are usually found in deep water (50 fathoms or more), occasional individuals (nearly always half-breeds) occurred in relatively shallow water in the fall of 1950. In addition to the female mentioned, 3 other female and 2 male siscowets were included in a total catch of 81 fish on that date. Of 879 fish caught August 11-November 8, 1950, off Ontonagon, Keweenaw Point, Marquette, and Munising, at depths of 4 to 35 fathoms, 22 (2.5 percent) were siscowets. Of these only 1 male, and the female mentioned above, were sexually mature.

Of great interest in Table 9 are the small mature female siscowets—much shorter than the smallest mature female lake trout collected. These short siscowets were caught about 45 miles north of Grand Marais, Michigan, (Station 16, Fig. 1) on September 28, 1954. The smallest, 16.8 inches long and 1.9 pounds in weight, was 8.3 inches shorter and 3.9 pounds lighter than the shortest and the lightest mature female lake trout in 9 pre-spawning and spawning-run collections in southern Lake Superior in 1950. The catch also included an even smaller, nearly spent female, 16.5 inches long, and a 15.7-inch, 1.3-pound mature (ripe) male.

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[9] Although the siscowet was described as a new species (*Salmo siscowet*) by Agassiz (1850), and is now customarily given sub-specific rank, Jordan and Evermann (1911) and others have expressed doubt as to whether it should be regarded as a distinct species or subspecies.

TABLE 9.—*Egg production of siscowets collected in Lake Superior, 1950-1954*

Specimen number	Date of collection	Locality[1] of collection	Total length (inches)	Weight (pounds)	Percentage of weight composed by gonads	Number of eggs	Eggs per pound of fish	Diameter of eggs[2] (millimeters)	*C*
1	Sept. 28, 1954	16	16.8	1.9	13.9	1,207	635	5.0	40.9
2	do.	16	17.3	2.2	11.1	1,093	497	5.0	42.9
3	do.	16	18.0	2.5	11.9	1,211	484	5.3	42.9
4	do.	16	20.1	3.5	3.5	1,220	346	3.9	43.5
5	Sept. 16, 1950	1	22.9	4.5	5.4	1,628	362	4.4	37.5
6	Sept. 28, 1954	16	25.3	8.3	3.5	3,861	465	3.6	51.5
7	Nov. 22, 1950	11	25.5	....[3]	....	2,859	...	4.9	....
8	Sept. 28, 1954	16	28.1	11.2	5.2	3,283	293	4.6	50.4
9	do.	16	29.1	12.5	3.4	8,243	659	3.4	50.7
10	Aug. 18, 1950	6	30.0	11.4	7.0	5,867	515	4.3	42.1
11	July 15, 1953	3	30.0	16.2	11.1	7,119	439	5.2	60.2
12	Sept. 28, 1954	16	32.1	20.2	10.0	7,435	368	5.3	60.9
13	July 25, 1950	9	34.2	20.3	13.0	10,476	516	5.4	50.7

[1] Locality refers to station number, Fig. 1, pp. 49
[2] Average diameter of 25 eggs taken at random from the preserved ovary
[3] Not weighed

Six fish of each sex were mature in a group of 13 males 15.7–20.9 inches in length and 16 females 16.5–20.8 inches long. Siscowets of this collection, therefore, matured at a much smaller size than did the lake trout of southern Lake Superior.

Despite irregularities, egg production of siscowets tended to increase with increasing length and weight of the fish. Egg numbers ranged from 1,093 in a 17.3-inch fish (No. 2) to 10,476 in a 34.2-inch specimen (No. 13). Production of eggs per pound fluctuated widely and was not correlated with length or weight of the fish. It ranged from 293 eggs per pound in a 28.1-inch fish (No. 8) to 659 in a fish (No. 9) 1.0 inch longer and 1.3 pounds heavier. Average egg production was identical (465 per pound) for 6 fish 25.3 inches or less in length and 6 fish 28.1 inches long or longer. This value is 28 percent less than the grand average egg production (646 eggs per pound) of lake trout of southern Lake Superior (Table 8).

In the graphical presentation of the data on egg production of siscowets (Figs. 2 and 3), no appreciable increase in the number of eggs occurred between lengths of 16.8 and 20.1 inches and weights of 1.9 and 3.5 pounds. From this point the numbers of eggs rose gradually in both graphs. The regression of number of eggs on length (Fig. 2), was similar for lake trout and siscowets. Of 8 siscowets within the range of lengths for which data were available for lake trout, 5 were close (within 600 eggs or less) to the curve drawn for egg production of lake trout. The other 3 were somewhat above the curve, but only 1 was outside the range of variation shown for individual lake trout of about the same length. Seven siscowets between the weights of 8.3 and 20.3 pounds (Nos. 6 and 8–13 of Table 9) showed not only a lower average egg production than did lake trout of comparable weights, but also a lower rate of increase in egg production with increasing weight (Fig. 3).

Milner (1874) found egg production of Lake Superior siscowets to range from 2,796 to 3,756 in 3 fish, and Eddy and Surber (1947) reported an average of 5,000 eggs in 4 females collected off Grand Marais, Minnesota, on July 10, 1938.

In the siscowets (Table 9) as among lake trout (Table 4) the percentage of total weight composed by the ovaries and egg diameter were closely correlated. The egg diameters averaged 5.2 millimeters among the 6 siscowets in which the ovaries made up 10 percent or more of the total weight; 4.4 millimeters for the 3 fish with percentages between 5 and 10; and 3.6 millimeters for the 3 fish with percentages less than 5. The poor correlation between the percentage of the total weight composed by the gonads (or egg diameters) and date of collection in the fish of Table 9 provides strong evidence that the siscowet has an extended spawning season. Two specimens (Nos. 1 and 9), both collected on September 28, 1954, in the same nets, represented the extremes for the series in percentage of the total weight composed by the ovaries (13.9 and 3.4 percent) and a wide divergence in average egg diameters (5.0 and 3.4 millimeters). The first of these fish was nearly ripe whereas the ovaries of the second were green. Two fish, 16.5 and 17.8 inches long which had already spawned (48 and 14 residual eggs, respectively) were collected on the same date. The ovaries of 2 fish (Nos. 13 and 11) collected on July 25, 1950, and July 15, 1953, were nearly ripe. Although the organs were complete and intact as removed from the fish, eggs were loosely attached and some fell from the preserved ovaries as they were being weighed. The organs had the appearance of nearly ripe lake trout ovaries during the height of the spawning season. Average egg diameters were 5.4 and 5.2 millimeters, respectively. At the other extreme, a siscowet (No. 7) collected November 22, 1950, had not yet spawned, although the diameter of its eggs (4.9 millimeters) indicated that it may have been nearing a ripe condition.

The data of Table 9 permit the assumption that spawning of siscowets may begin by late July and extend at least to late November. An even wider divergence for siscowets (or lake trout) is indicated by the collection on June 8, 1953, of 3 females from 19.4 to 23.4 inches long off Gull Island, near the eastern extremity of Isle Royale (Station 2, Fig. 1). One fish was nearly ripe and 1 was nearly spent. Ripe fish of both sexes were reported by Emil Tormala, the commercial fisherman who made the collections and who fished on this reef during three successive annual spawning runs. The fish were caught at depths of 8 to 15 fathoms, within a few hundred feet of water 75 to 100 fathoms deep. They are known by fishermen as "humpies", and are presumably from a local race, whose affinities with lake trout or siscowets were undetermined.[10] This and the other collections discussed above are the basis for the statement that siscowets or lake trout may spawn in Lake Superior during at least 6 months of the year (June to November).

This wide spread in spawning times corroborates statements of other workers. Milner (1874) noted that spawn in some siscowets was ripe and running freely by the latter part of August and that in September the females were all ripe and depositing spawn. Eddy and Surber (1947) reported the capture of a ripe female and male off Knife River, Minnesota, on November 29, 1923.

The capture of nearly ripe and spent siscowets on September 28, 1954, at depths of 50 to 80 fathoms tends to confirm the statement by Milner (1874) that they have no migratory instinct at this season, but are taken while spawning in the same locality where they were taken previously.

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[10] Analyses of flesh samples from the 3 "humpies" collected on June 8, 1953, and from a series of "leans" and siscowets collected in Lake Superior in 1953 and 1954, were completed by Arthur M. Phillips, Jr., after this paper had been submitted to the printer. Determinations by ether extraction indicated that each of the 3 fish had fat contents well within the range for siscowets, and much greater than that for lean trout of this size. "Humpies" are thus presumed to represent a race of early spawning siscowets.

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THE PYGMY WHITEFISH, *COREGONUS COULTERI,* IN LAKE SUPERIOR

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Abstract

Bottom trawling by the U. S. Fish and Wildlife Service motor vessel *Cisco* in Lake Superior in 1952–1953 revealed a large population of a tiny whitefish, *Coregonus* (*Prosopium*) *coulteri,* which has been reported previously only from northwestern North America. The hiatus in range, from Lake Superior to the

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Columbia River basin, is the greatest known for a North American freshwater fish. Although minor structural differences characterize the disjunct populations of the pygmy whitefish, these are not deemed worthy of nomenclatorial recognition. Comparisons with related species indicate that the pygmy whitefish is distinctive in the small size, large scales, few vertebrae, few pyloric caeca, and in other characters.

The pygmy whitefish is widely distributed in Lake Superior, especially in semi-protected bays, such as Keweenaw Bay which yielded about 68 percent of the 1,623 specimens caught. The bathymetric range was 10 to 49 fathoms, with maximum abundance at the 25- to 39-fathom interval. Average length of fish increased progressively with water depth, chiefly because the number of yearlings declined from 100 percent at 10–14 fathoms to none at 45–49 fathoms.

The average total length of pygmy whitefish caught by trawling was 3.4 inches (range 1.2 to 5.7). Extraordinarily slow growth was revealed by the examination of scales. Two fish from Keweenaw Bay, both nearing the end of their eighth growing season, were only 5.4 inches long. Compared to Keweenaw Bay, growth rate was about the same near Laughing Fish Point, faster in the Apostle Islands (and in Bull and McDonald Lakes, Montana), and slower in Siskiwit Bay, Isle Royale. Females grew more rapidly than males after the second year and had a longer life span.

All male pygmy whitefish were mature at the age of 2 years and a total length of 3.6 or more inches. Most females were mature at 3 years and 4.2 inches; all older females were mature. Mean egg production was 362 (range, 93 to 597) per fish and 26 per gram of total weight for fish from 3.4 to 5.9 inches long. Spawning in 1953 occurred sometime in November or December.

Crustacea (principally ostracods and amphipods—copepods in the young) occurred in 106 of 112 pygmy whitefish stomachs and made up 77 percent of the total food volume. When available, fish eggs appear to be important in the diet.

Other cold-water fishes—cottids, ninespine sticklebacks, smelt, and four species of coregonines—were the most frequent associates of the pygmy whitefish. Lake trout and trout-perch were also taken with it at the same stations or in the same trawl hauls. Its closest relative in Lake Superior, the round whitefish, was not an ecological associate.

INTRODUCTION

One of the most comprehensive studies yet attempted on a sizable group of fishes over a considerable region, the monograph of the whitefishes of the Great Lakes (Koelz, 1929), presented a wealth of information on the taxonomy, morphometry, areal and bathymetric distribution, size, abundance, breeding habits, and variation of the 11 species known from the area. The possibility that any species was overlooked in this survey seemed remote. Yet the introduction of bottom trawling by the U. S. Fish and Wildlife Service motor vessel *Cisco* in 1952–1953 revealed an abundant population of a tiny whitefish, *Coregonus coulteri*, in Lake Superior. The small size accounts for the failure of earlier investigators to collect it, since this whitefish is not vulnerable to the commercial gill or impounding nets that are fished where it lives. The bathymetric distribution, from about 10 to 49 fathoms, accounts for the failure of the species to appear in shore collections taken with small-mesh gear.

The discovery of pygmy whitefish in Lake Superior is particularly fascinating because all previous records of occurrence are from the Pacific slope. The present new record reveals a gap of roughly 1,100 miles in the distribution. No other freshwater or terrestrial vertebrate (birds excepted) in North America is known to us to display such a strikingly disjunct range. In reporting the discovery of the species in Lake Superior we have felt impelled to compare this stock carefully with that from the Pacific slope. In addition, we contrast it with its closest relative in the Great Lakes basin, the round whitefish, *Coregonus cylindraceus* (termed *Prosopium quadrilaterale* by Koelz), and present information on occurrence within the lake, bathymetric distribution, size, growth, reproduction, food, and associates.

MATERIALS AND METHODS

Pygmy whitefish were collected at 17 stations in Lake Superior (Table 1; Fig. 3) by dragging an otter trawl along the lake bottom. Most were caught in nets 35 feet wide at the wings and 36 feet long. Mesh sizes of the cotton netting ranged from 1½ and 2½ inches (extension measure) at the forward end to ½ inch at the cod end. Ordinarily the trawl was lowered to the bottom, towed for 10 minutes (usually parallel to the contour), and then retrieved. Water depth over the area trawled was recorded by a fathometer, and station locations were determined by radar.[1] The distance covered in a 10-minute haul depended partly on prevailing winds and currents, but probably averaged about ½ mile. Fish caught were preserved in formalin immediately after collection. All measurements and weights given in this paper were made after preservation.

Morphometric measurements and counts have mostly been taken as described by Koelz (1929, pp. 305–308). Head length, as measured, includes the opercular membrane. The upper-jaw length was measured from the tip of the snout, apparently in the same way as Koelz measured the "maxillary." An orbital diameter is employed to replace the eyeball measurement used by Koelz. All rudimentary gillrakers are included in the count. Lateral-line scales were counted to the base of the caudal fin, irrespective of the position of the last pored scale; this count is not exactly equivalent to Koelz' method. For fin-ray counts all elements in the pectoral and pelvic fins are included. The last ray of the dorsal and anal fins is counted as double at the base (as recorded also by Koelz), but all anterior elements are included, no matter how short; thus the counts are taken in the same manner as by Dymond (1943) but are two or three higher than Koelz' tabulations, in which the first ray approached three-fourths the length of the longest ray in the fin. Unbranched and branched rays are segregated, then summed (*e.g.*, iii + 8 = 11). The number and lengths of the unbranched rays in these fins vary erratically, and enumeration of all rays provides the most stable, hence probably the most reliable, count.

In addition to the Lake Superior specimens we have examined the following material of *Coregonus coulteri:*

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[1] A description of the *Cisco* and its navigational and research equipment was given by Moffett (1954).

TABLE 1. — *Collection localities for the pygmy whitefish in Lake Superior, 1952-1954*

[See Figure 3 for location of stations]

General locality	Station	Latitude	Longitude	Date	Depth (fathoms)	Time trawled (minutes)	Number of fish	Total length[1] (millimeters)
Wisconsin								
North of Apostle Islands	1	47° 09′ 15″	90° 30′ 00″	Aug. 20, 1952	32-33	8	1	122
Apostle Islands	2	47° 00′ 30″	90° 47′ 50″	July 28, 1953	6-16	47	2	72-126
Apostle Islands	3	46° 54′ 15″	90° 35′ 30″	May 30, 1953	11-46	60	26	93-146
				July 29, 1953[2]	30-32	...[3]	6	143-149
Apostle Islands	4	46° 46′ 50″	90° 49′ 15″	July 30, 1953	22	10	1	116
Apostle Islands	5	46° 48′ 40″	90° 38′ 35″	July 30, 1953	8-19	28	1	98
Michigan								
Siskiwit Bay, Isle Royale	6	47° 54′ 40″	88° 57′ 00″	Sept. 7, 1953	14-38	52	108	32-108
				Sept. 30, 1953	13-18	20	266	35- 91
Northeast of Grand Traverse Bay	7	47° 12′ 30″	88° 08′ 00″	July 9, 1953	11-25	30	4	61- 72
Northeast of Keweenaw Bay	8	47° 05′ 30″	88° 10′ 00″	May 7, 1953	31	6	7	88-136
Western Keweenaw Bay	9	47° 03′ 00″	88° 20′ 45″	July 8, 1953	18-28	40	111	62-121
				Sept. 5, 1953	10-17	29	2	31- 72
				Oct. 3, 1953	15-23	30	22	70- 85
Western Keweenaw Bay	10	46° 59′ 30″	88° 22′ 00″	July 8, 1953	15	10	12	54- 73
Southern Keweenaw Bay	11	46° 48′ 21″	88° 26′ 55″	May 11, 1953	39-50	129	4	104-123
				July 11, 1953	27-33	30	83	65-134
				Aug. 2, 1953	10-42	120	188	62-134
				Sept. 11, 1953	13-43	114	345	61-141
				Oct. 2-3, 1953	14-32	43	71	67-133
				Oct. 15, 1953	14-45	135	252	59-140
Eastern Keweenaw Bay	12	46° 53′ 30″	88° 21′ 35″	July 11, 1953	10-18	65	9	65- 74
Off Point Abbaye	13	46° 58′ 45″	88° 07′ 30″	Sept. 10, 1953	10-17	35	6	31- 80
Northeast of Point Abbaye	14	47° 03′ 00″	88° 04′ 55″	Aug. 16, 1952	34-55	9	20	90-140
East of Marquette	15	46° 34′ 10″	87° 12′ 50″	Aug. 12, 1953	42	6	1	126
Laughing Fish Point	16	46° 31′ 20″	86° 55′ 30″	July 13, 1953	18-19	50	1	74
				July 22, 1953	16-18	35	1	64
				Aug. 12, 1953	11-22	42	2	61- 63
				Sept. 14, 1953	13-39	120	34	33-109
				Oct. 5, 1953	15-30	50	19	40- 84
				Oct. 21-22, 1953	13-40	103	10	47-124
				Jan. 11, 1954	43-54	40	5	94-127
Ontario								
North of Whitefish Bay	17	46° 56′ 40″	84° 46′ 25″	Aug. 19, 1953	27-28	20	3	84- 90

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[1] Range in length refers only to specimens which were preserved; 96 fish were discarded at the time of collection

[2] Three tiny coregonines, 27 to 29 millimeters in total length that were caught by trawling on July 29 at 5 to 9 fathoms, about 10 miles northeast of Station 3, were probably pygmy whitefish. Since identity is not certain, however, they are not considered elsewhere in this paper

[3] Nylon gill nets, 1-inch mesh (extension measure)

UMMZ [2] 167,941, here designated as lectotype of *Coregonus coulterii* Eigenmann and Eigenmann, a tuberculate, adult male, 92.5 millimeters in standard length, collected in the Kicking Horse River, elevation 4,050 feet, Columbia River system, at Field, British Columbia, by Carl H. Eigenmann in 1892. (Data on the lectotype are given in Table 2.) This specimen together with four others, UMMZ 61,949, was formerly catalogued as Indiana University 4,446. Eigenmann's original collection consisted of over 100 syntypes. Others seen by us are USNM 44,875 (3 specimens) and USNM 64,089 (1). One specimen is now in the British Museum (Dymond, 1943, p. 203) and 7 are in the Stanford collection (Böhlke, 1953, p. 13). Although Evermann and Smith (1896, p. 290) and subsequent authors have specified USNM 44,875 as "type" of *C. coulteri,* this action does not constitute valid designation of a lectotype (Int. Comm. Zool. Nomen., 1953, pp. 72–77) since the lot referred to includes three specimens, as noted by Böhlke (1953).

USNM 126,910 (3), Lake Aleknagik, Alaska, August 2, 1911, G. Dallas Harma and July 20, 1909, M. C. Marsh.

SU 24,809 (1), Chignik River near weir, Alaska, June 11–19, 1928, Harlan B. Holmes.

SU 24,810 (3), Upper Chignik River, Alaska, June 7–8, 1928, H. B. Holmes.

SU 24,811 (12), Chignik River at coal mine, Alaska, August, 1924, Charles Petry.

BC, 54–423 (2), Lower Arrow Lake, sandy point opposite Renata, British Columbia, June 26, 1949, T. G. Northcote.

SU 5,477 (2), Diamond Lake, Pend Oreille County, Washington, June, 1894, J. O. Snyder. Diamond Lake was said by Snyder (1917) to be located in Stevens County, Washington, a statement repeated by other workers. There is a Diamond Lake in Pend Oreille County, and Clarence F. Pautzke, Chief, Fishery Management Division, Washington Department of Game, confirms our suspicion that this must be the lake intended.

MSU W53-2 (5) and UMMZ 167,942 (5), mouth of Ross Creek, Bull Lake, tributary to Kootenai River, near Troy, Lincoln County, Montana, December 26, 1952, J. B. Dillon.

MSU W53-3 (7) and UMMZ 167,943 (6), same locality, January 12, 1953, Kenneth Hays.

USNM 104,688 (2) mouth of Fish Creek, Lake McDonald, Glacier National Park, Montana, August 25, 1935, L. P. Schultz and A. S. Hazzard.

USNM 101,606 (4), near mouth of McDonald Creek, Lake McDonald, Glacier National Park, Montana, probably late November 1935, C. L. Croghan.

USNM 102,375 (37), Lake McDonald, Glacier National Park, Montana, November 17, 1936, C. L. Croghan.

GENERIC PLACEMENT

European ichthyologists have long and consistently grouped the whitefishes other than *Stenodus leucichthys* in the single genus *Coregonus.* North American authors, in contrast, have for the most part adopted the segregation advocated by Koelz (1929) into three genera—*Leucichthys, Coregonus,* and *Prosopium.* Koelz keyed out the species (and genera) of whitefishes in each of the Great Lakes, defined the characters of each genus on the basis of the species present in that region, and evaluated the principal characters employed in whitefish taxonomy, again confining his critique to local species. Nowhere did he include extralimital forms in a clear definition of the genera. The differences between genera as stated may seem adequate, but each of two of the "genera" was represented by a single species then known in the Great Lakes fauna. How tenuous was the basis for the segregation of *Prosopium* may be illustrated by consideration of the characters of the pygmy whitefish. Koelz (1929) distinguished *Prosopium* (*quadrilaterale*) from the other whitefishes of Lake Superior in several characters. The pygmy whitefish agrees with *Prosopium,* as defined, in the single narial flap, the lack of vestigial teeth on the jaws and the roof of the mouth (although lingual teeth are present), the number of gillrakers, and the subterete body. *C. coulteri* agrees with *Leucichthys* and *Coregonus* but differs from *Prosopium* in the size of the exposed field of the lateral-line scales (not conspicuously smaller than the adjacent rows); fits *Coregonus* better than *Prosopium* in shape of snout, size of upper jaw, length of mandible, ratio of pelvic length to pelvic-anal distance, and presence of nuptial tubercles on the head; and is intermediate between *Prosopium* and *Coregonus* in gillraker length. In our judgment the morphological basis for segregation of genera becomes untenable if extralimital species, which reduce even further the utility of the differentiating characters, are included. We, therefore, agree with the generic nomenclature of Berg, Järvi, Regan, Svärdson, Thienemann, and other European investigators, and with those recent American and Canadian ichthyologists (*e.g.*, Shapovalov and Dill, 1950; Legendre, 1954; Wilimovsky, 1954) who have of late employed *Coregonus* (*sensu lato*). Also, we follow Regan (1914) and Berg (1940) in assigning the whitefishes to a subfamily, Coregoninae, of the Salmonidae.

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[2] Abbreviations for museum specimens are as follows: BC, University of British Columbia; MSU, Montana State University; SU, Museum of Natural History, Stanford University; UMMZ, Museum of Zoology, University of Michigan; USNM, United States National Museum.

Coregonus (*Prosopium*) *coulteri* Eigenmann and Eigenmann—Pygmy Whitefish

Coregonus coulterii.—Eigenmann and Eigenmann [not E. and G.—a typographical error], 1892, pp. 961–963 (original description; Kicking Horse River, 4,050 feet, Field, British Columbia). Evermann and Smith, 1896, pp. 288, 290–291 (description and comparisons; pl. 12; Kicking Horse River, Field, B. C.). Jordan and Evermann, 1896–1900, pp. 462–463, pl. 76 (compiled). Halkett, 1913, p. 48 (compiled). Cockerell, 1913, pp. 125–126 (scales).

Coregonus coulteri.—Eigenmann, 1894, pp. 105, 115, 119, 121, 132, pl. 6 (description; Kicking Horse River, Field and Golden, B. C.). Evermann and Goldsborough, 1907, p. 99 (compiled). Jordan and Snyder, 1909, p. 430 (comparisons; Diamond Lake [Pend Oreille Co.], Washington). Jordan and Evermann, 1911, p. 41, fig. (compiled). Kendall, 1917 (description; Second Lake and stream connecting it with First Lake, Chignik [Alaska Peninsula], Alaska). Snyder, 1917 (preyed upon by kingfishers; Diamond Lake, "Stevens Co.," Washington). Snyder, 1919, p. 4 (compiled). Kendall, 1921 (size [maximum total length 198 millimeters]; description; food; Lake Aleknagik, Alaska). Wilimovsky, 1954, p. 282 (range).

Prosopium coulteri.—Jordan, Evermann, and Clark, 1930, p. 65 (compiled). Schultz, 1936, p. 139 (comparisons; range). Schultz, 1941, pp. 8, 24–25, 39, fig. (characters; Fish Creek and McDonald Creek, tributaries to Lake McDonald, Glacier National Park, Columbia River basin, Montana). Wynne-Edwards, 1952, p. 16 (Sockeye Lake on the upper Alsek, 60°30′N., 137°38′W., Yukon Territory; records compiled). Weisel and Dillon, 1954, pl. 1 (characters; natural history; Bull Lake, Lincoln Co., Montana).

Prosopium coulterii.—Myers, 1932 (comparisons; Kicking Horse River, Field, British Columbia; Diamond Lake, Washington; Chignik River, Alaska).

Dymond, 1943, p. 202–203 (characters). Dymond, 1947, p. 8 (characters; records, including Yukon [Territory]). Carl and Clemens, 1948 (and 1953), p. 35, figs. (compiled).

Prosopium snyderi.—Myers, 1932 (original description; figure; holotype, SU 23,751, Crescent Lake, Olympic Peninsula, Washington). Schultz, 1936, p. 139 (comparisons; Lake Crescent, Olympic Peninsula, Washington). Myers, in Böhlke, 1953, p. 14 ("Crescent Lake may not have been the one on the Olympic Peninsula").

Coulter's whitefish.—Wynne-Edwards, 1947, pp. 12, 19 (Sockeye Lake, Alsek River system, Yukon Territory).

NOMENCLATURE

The original specific name *coulterii* is emended to *coulteri* in accordance with the recent decisions on patronymics established by the International Commission on Zoological Nomenclature (1953).

As indicated in the above synonymy, the type locality of *Prosopium snyderi* Myers cannot now be located with certainty. It is clear from the original account that this nominal species is close to *C. coulteri. P. snyderi* was said to differ from *coulteri* principally in certain body proportions, notably the longer fins, and in the larger scales. The lateral-line scale count, however, is well within the limits of variation for *coulteri,* as are most of the proportional measurements (Table 2). Sex dimorphism, especially in length of the fins, seems to account for the differences noted by Myers between *snyderi,* the male (as checked for us by N. J. Wilimovsky), and *coulteri,* the female (all specimens from the Chignik River, including the fish figured by Myers, are females). Since there remains no adequate basis for specific separation, *Prosopium snyderi* is placed in the synonymy of *C. coulteri.*

The Committee on Names of Fishes has expressed its disapproval of patronymics (*e.g.,* Coulter's whitefish) as common names (Transactions of the American Fisheries Society, Vol. 84. Of the two alternative names suggested for the species we prefer pygmy whitefish to brownback whitefish as being briefer, more suitably descriptive, and more euphonious. The name pygmy whitefish was introduced by Weisel and Dillon (1954).

DESCRIPTION

Diagnosis.—Coregonus coulteri (Fig. 1) agrees with other species of the subgenus *Prosopium* in having a single internarial flap, in the presence of parr markings on the body in the young, in lacking teeth on the jaws, vomer and palatine, and in the terete body. The anterior lateral-line scales have the exposed field subequal to or only slightly smaller than the adjacent body scales. The scales are large, 54 to 70 along the lateral line, 31 to 40 around the body, and 16 to 20 around the caudal peduncle; dorsal rays 10 to 14; pyloric caeca 15 to 23; vertebrae 52 to 54. The mouth is subterminal, the premaxillae are inclined downward and backward, and sometimes are almost vertical. The gillrakers number 13 to 20, and are short to moderate in length, measuring from 1.3 to 2.1 percent of the standard length. The snout is broadly rounded in dorsal view. The mouth is of

TABLE 2. — *Proportional measurements of* Coregonus coulteri, *expressed in thousandths of standard length*

[Data for the holotype of *Prosopium snyderi* are calculated from Myers (1932)]

Measurement	Lectotype[1]	Holotype,	Bull Lake, Montana				Keweenaw Bay, Michigan			
	C. coulteri	*P. snyderi*	5 males		2 females		5 males		5 females	
			Range	Mean	Range	Mean	Range	Mean	Range	Mean
Standard length (millimeters)	92.5	137.0	86-109	98	118-128	123	88- 96	92	100-111	104
Dorsal origin to snout tip	465	467	438-486	463	453-463	458	470-480	474	467-483	477
Dorsal origin to caudal base	551	...	546-555	551	556-566	561	523-551	540	528-548	536
Dorsal origin to adipose origin	347	...	345-371	358	362-382	372	314-341	333	325 344	333
Pelvic insertion to snout tip	491	511	495-529	510	494-501	498	493-515	502	499-531	514
Pelvic insertion to caudal base	523	...	495-508	500	508-512	510	502-522	511	477-498	489
Pelvic insertion to anal origin	257	...	229-245	238	244-257	250	231-249	237	220-236	228
Body depth	172	212	180-199	187	178-206	192	188 219	200	199-225	212
Body width	...	...	101-113	108	107-134	120	98-113	106	111-128	118
Caudal peduncle length	176	153	151-167	160	166-168	167	153-182	170	145-176	163
Caudal peduncle depth	63	73	65- 71	69	62- 75	68	72- 77	74	67- 78	73
Head length	230	248	234-255	244	223-233	228	240-250	245	238-244	240
Head depth	132	153	135-143	140	131-137	134	123-134	128	130-149	141
Interorbital width	53	55	54- 58	56	55- 58	56	46- 50	48	45-50	47
Snout length	58	66	56- 64	60	56- 60	58	54- 60	57	58- 61	59
Orbit length	68	62	68- 79	74	63- 66	64	67- 75	70	65- 72	69
Upper jaw length	65	55	65- 70	67	55- 60	58	70- 73	71	67- 71	69
Lower jaw length	80	...	84- 91	87	81- 83	82	93-100	97	86- 92	90
Dorsal fin height	192	219	212-221	217	190-212	201	181-214	196	170-192	184
Adipose fin length	86	...	83-101	90	94- 96	95	81- 96	88	83- 91	88
Anal fin height	184	197	173-203	186	165-172	168	160-163	161	141-156	147
Caudal fin length	...	...	260-278	267	247-266	256	217-236	229	205-231	213
Pectoral fin length	197	234	194-200	198	177-193	185	171-190	183	160-173	165
Pelvic fin length	179	197	171-178	176	159-170	164	154-172	164	142-159	152
Gillraker length	13	...	17- 21	18	16- 18	17	15- 17	16	14-16	15

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[1] The lectotype has 11 dorsal rays (3 simple), 13 anal rays (4 simple), 16-16 pectoral rays, 10-9 pelvic rays, 59 scales along lateral line, 35 scales around the body in front of the dorsal fin, of which 14 are above the lateral lines and 19 below, 18 scales around the caudal peduncle, of which 8 are above and 8 below the lateral lines, and 5 + 1 + 9 = 15 gillrakers

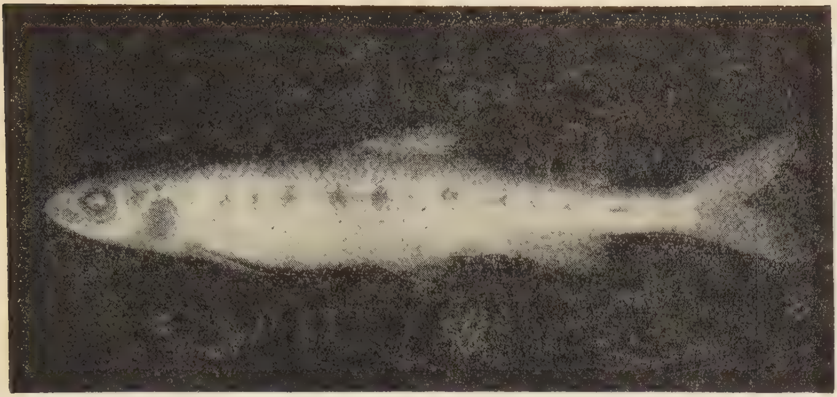

FIGURE 1.—*Coregonus coulteri,* a mature female, 4.8 inches long and 4 years old, collected October 15, 1953, in Keweenaw Bay, Lake Superior.

moderate size. The maximum total length recorded is less than 8 inches.

Description of Lake Superior stock.—Body proportions are presented in Table 2 and fin-ray, scale, and gillraker counts are given in Tables 3-7. *Coregonus coulteri* (Fig. 1) is apparently the smallest species of the genus; the largest specimen obtained in Lake Superior was 149 millimeters in total length although somewhat larger fish have been taken in the Pacific drainage (see Tables 15 and 17 for length distribution and size at maturity).

In measured specimens of the pygmy whitefish, females have large eggs and the body averages deeper and broader than in males (Table 2). The only other parts in which marked sex dimorphism is evident are the lengths (and heights) of the rayed fins; in all of these the males have the greater

TABLE 3. — *Frequency distributions of counts of dorsal and anal fin rays in* Coregonus coulteri

[All unbranched rays are included. N = number of specimens]

Locality	Dorsal rays					N	Mean	Anal rays					N	Mean
	10	11	12	13	14			11	12	13	14	15		
Alaska														
Lake Aleknagik	..	..	3	..	..	3	12.00	..	2	1	..	..	3	12.33
Chignik River	..	8	7	1	..	16	11.56	..	6	8	2	..	16	12.75
Columbia drainage														
Kicking Horse River	..	5	4	..	..	9	11.44	1	2	5	1	..	9	12.67
Lower Arrow Lake	..	1	1	..	..	2	11.50	..	1	1	..	..	2	12.50
Diamond Lake	..	2	..	..	..	2	11.00	..	1	1	..	..	2	12.50
Bull Lake	..	7	13	3	..	23	11.83	1	10	10	2	..	23	12.57
Lake McDonald	..	14	5	..	1	20	11.40	1	12	5	1	1	20	12.45
Lake Superior	5	23	2	..	..	30	10.90	..	1	18	6	..	25	13.20

TABLE 4. — *Frequency distributions of counts of pectoral and pelvic fin rays in* Coregonus coulteri

[Counts for right and left sides are summed. N = number of specimens]

Locality	Pectoral rays									N	Mean	Pelvic rays					N	Mean
	26	27	28	29	30	31	32	33	34			18	19	20	21	22		
Alaska																		
Lake Aleknagik	..	..	1	1	1	..	..	..	..	3	29.00	..	1	2	..	..	3	19.67
Chignik River	..	..	1	2	6	4	3	..	..	16	30.38	4	4	6	1	..	15	19.27
Columbia drainage																		
Kicking Horse River	..	..	..	..	6	..	3	..	..	9	30.67	2	2	5	..	..	9	19.33
Lower Arrow Lake	..	..	..	..	..	2	..	..	..	2	31.00	1	..	..	..	1	2	20.00
Diamond Lake	..	..	..	..	2	..	..	..	..	2	30.00	..	1	1	..	..	2	19.50
Bull Lake	..	..	..	1	3	4	10	2	3	23	31.78	..	1	22	..	..	23	19.96
Lake McDonald	..	..	..	..	1	7	6	3	3	20	32.00	3	7	10	..	..	20	19.35
Lake Superior	1	1	4	8	8	2	1	..	..	25	29.24	..	2	13	4	6	25	20.56

TABLE 5. — *Frequency distribution of lateral-line scale counts in* Coregonus coulteri

[N = number of specimens]

Locality	Lateral-line scales																	N	Mean
	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70		
Alaska																			
Lake Aleknagik	..	..	..	..	..	..	..	..	..	1	..	..	..	..	..	..	2	3	67.67
Chignik River	..	..	..	..	1	..	1	2	2	..	4	2	2	..	1	..	1	16	63.75
Columbia drainage																			
Kicking Horse River	..	..	..	1	..	3	..	..	3	..	2	..	..	..	..	..	..	9	60.89
Lower Arrow Lake	..	1	..	..	1	..	..	..	..	..	..	..	..	..	..	..	..	2	56.50
Diamond Lake	..	..	..	..	1	..	..	..	..	..	1	..	..	..	..	..	..	2	61.00
Bull Lake	..	..	..	1	2	4	4	3	4	4	1	..	..	..	..	..	..	23	60.70
Lake McDonald	..	..	4	2	4	2	2	2	1	1	1	1	..	..	..	..	..	20	59.20
Lake Superior	2	6	5	4	4	5	..	2	1	..	..	..	..	..	..	..	..	29	57.14

dimensions (Table 2). The increased size is presumably of adaptive significance since in breeding males (from Montana) these fins (as well as the head and body) are well supplied with nuptial tubercles; it is surmised that the fins function in the spawning embrace.

Like most other species of the subgenus *Prosopium*, *Coregonus coulteri* is terete; the body width is decidedly more than half the depth. Several related species (*e.g.*, *C. cylindraceus*, *C. williamsoni*) have the snout notably shortened and conical, more or less sharply angulate in dorsal aspect (Koelz, 1929, p. 323, Fig. 12), in contrast to the bluntly rounded snout of the lake whitefish, *Coregonus clupeaformis*, and the size of the mouth is much smaller than in *clupeaformis*. The profile of the snout in *coulteri* is similar to that of *clupeaformis*, and the mouth is about the same size. The upper jaw of *coulteri* is contained in the head length 3.1-3.4 times (2.9-3.6 in *clupeaformis* from Lake Superior—data from Koelz, 1929); the

TABLE 6. — *Frequency distributions of body-circumference and caudal-peduncle scales in* Coregonus coulteri

[N = number of specimens]

Locality	Body-circumference scales										N	Mean	Scales around caudal peduncle					N	Mean
	31	32	33	34	35	36	37	38	39	40			16	17	18	19	20		
Alaska																			
Lake Aleknagik.....	..	..	..	1	..	2	..	..	..	..	3	35.33	..	..	..	..	3	3	20.00
Chignik River.......	..	..	2	9	2	2	1	..	..	..	16	34.44	1	1	13	1	..	16	17.88
Columbia drainage																			
Kicking Horse River.	..	..	..	..	3	..	3	1	1	1	9	37.00	..	2	5	2	..	9	18.00
Lower Arrow Lake...	..	1	..	..	1	..	..	..	..	..	2	33.50	..	..	2	..	..	2	18.00
Diamond Lake......	..	..	1	..	1	..	..	..	..	..	2	34.00	..	..	2	..	..	2	18.00
Bull Lake...........	..	..	5	2	9	6	1	..	..	..	23	34.83	..	1	11	8	2	22	18.50
Lake McDonald.....	1	1	6	8	3	..	..	..	..	..	19	33.58	..	2	11	5	2	20	18.35
Lake Superior.........	..	..	3	1	5	7	2	3	..	..	21	35.62	..	..	3	7	14	24	19.46

TABLE 7. — *Frequency distribution of gillraker counts in* Coregonus coulteri

[Rudimentary rakers are included. N = number of specimens]

Locality	Number of gillrakers								N	Mean
	13	14	15	16	17	18	19	20		
Alaska										
Lake Aleknagik..................	2	..	1	..	..	..	..	..	3	13.67
Chignik River......................	3	5	5	2	1	..	..	..	16	14.56
Columbia drainage										
Kicking Horse River...............	..	1	5	3	..	..	..	..	9	15.22
Lower Arrow Lake................	1	1	..	..	..	..	..	..	2	13.50
Diamond Lake.....................	..	..	..	1	1	..	..	..	2	16.50
Bull Lake..........................	..	..	2	6	10	2	1	..	21	16.71
Lake McDonald....................	..	..	2	5	5	3	5	..	20	17.20
Lake Superior.......................	..	..	..	1	6	17	13	3	40	18.28

lower jaw is contained in the head 2.3-2.6 times (2.4-2.7 times in *clupeaformis*).

Both simple and branched rays of the dorsal and anal fins vary in number, and the arbitrary designation of the first ray on the basis of length is also unsatisfactory. There are usually 3, occasionally 2 or 4, unbranched dorsal rays, and usually 8, sometimes 7 or 9, branched rays; the total dorsal count is 10 to 12, usually 11 (Table 3). There are usually 3 or 4, occasionally 5, unbranched anal rays and 9 or 10, infrequently 8, branched rays; the total anal rays number (12) 13 or 14. All of 10 specimens counted had 19 principal caudal rays (17 branched). The pectoral rays vary from 13 to 16, and the pelvic rays from 9 to 11 (Table 4).

The scales are the largest in the family Salmonidae (Tables 5-6). The lateral-line scales number 54 to 62. There are 33 to 38 body-circumference scales, of which 13 to 15 are above the lateral lines and 18 to 23 are below.

The scales around the caudal peduncle number 18 to 20, of which 8 or 9 are above the lateral lines and 8 or 9 are below. The breast and belly are fully covered with scales equal in size to those on the remainder of the body. Unlike *Coregonus cylindraceus,* the scales of the lateral-line row have the exposed field equal to or scarcely smaller than the scales of adjacent rows.

The gillrakers are rather short (6.5 to 8.8 percent of head length, 1.4 to 1.7 percent of standard length) but are relatively longer than in *C. cylindraceus.* The rakers number 5 to 7 on the upper limb, 1 at the angle, and 10 to 12, most often 11, on the lower limb. Total raker counts (all rudiments included) vary from 16 to 20 (Table 7). The branchiostegal rays in 10 specimens counted number 7-7 in 3, 8-7 in 1, and 8-8 in 6.

The small number of pyloric caeca, perhaps the most distinctive structural feature of *Coregonus coulteri,* has apparently escaped prior notice. Ten Lake Superior specimens yield the following counts: 15 (1 specimen), 16 (2), 17 (2), 18 (2), and 19 (3). Three fish from Lake McDonald, Montana, have 20, 21, and 23 caeca. All caeca are simple. The minimum number of caeca for any other whitefish in the Great Lakes is 87 to 117 in *Coregonus cylindraceus* (Koelz, 1929). In vertebral count, too, the pygmy whitefish has a lower count than is usual among salmonids. Ten specimens have the following counts: 52 (2), 53 (7), 54 (1). The range of counts tabulated by Koelz (1929) among Great Lakes whitefishes is from 55 (in *C. zenithicus* and *C. hoyi*) to 63 (in *C. clupeaformis* and C. *cylindraceus*).

In adults the jaws, vomer, and palatine are toothless. The tongue, however, typically has several well developed, immovable teeth. These are imbedded but are readily revealed by removal of the soft tissue. Two large specimens of *coulteri* from Lake Aleknagik, Alaska, lack teeth on the tongue, but an individual from the Upper Chignik River, Alaska, has lingual teeth. Examination of several specimens of *Coregonus cylindraceus* from Lake Superior indicates the presence in this species also of one or a few teeth on the tongue. Koelz (1929) found no teeth in the mouth of this species.

In preservation *Coregonus coulteri* is pale tan, immaculate below and dusted lightly with melanophores on the lateral and dorsal surfaces of head and body. Along the lateral line is a series of about 8 to 11 subcircular parr marks that are more or less diffuse near their margins in half-grown individuals and become very indistinct in large adults (Fig. 1). The back is similarly marked by an irregular series of about 12 to 14 dark spots. A few additional spots are often present on the dorsolateral surface. There is a dark bar on the preorbital bone that parallels the upper jaw, and there are usually 1 to 3 dark spots on the top of the head behind the eyes.

Geographic variation.—In view of the great phenotypic and probably genotypic variability among whitefishes, it is to be anticipated that a species with a discontinuous range as extensive as that of the pygmy whitefish would exhibit notable local or regional variations in structure. Such observed variations have furnished the basis for the naming of a plethora of species and subspecies both in Eurasia and North America, with the addition of numerous infrasubspecies and even lesser named ranks among Old World coregonines. As expected, *Coregonus coulteri* is not structurally homogeneous throughout its range, but the strong similarity among the disjunct populations is more impressive than the relatively slight differences. Commonly the deviations present no consistent geographic pattern, giving rise to the suspicion that they are strictly local and represent genetic emphasis or reflect ecological differences rather than fundamental geographic divergence. More material, especially from the northwestern part of the range, is needed to resolve some aspects of the problem of geographic variation.

On the basis of the samples measured (Table 2), a number of body parts give evidence of variation. Notable among these are the lengths of the rayed fins, which also displayed sex dimorphism (p. 169). In each sex the fins of pygmy whitefish from Bull Lake, Montana, are higher (or longer) than those from Keweenaw Bay, Lake Superior. Only for the adipose fin do the differences seem to be of dubious reliability. The higher anal fin in the Bull Lake fish is especially notable. The type specimen of *Prosopium snyderi* is seen to agree closely with males of the Bull Lake stock in the dimensions of the median fins but has longer paired fins (it is possible that differences in mensural techniques are involved here). The lower jaw, and perhaps the upper jaw, average longer in the Lake Superior fish than in those from Bull Lake. The interorbital breadth is consistently greater in the Bull Lake whitefish. There are indications that the dorsal fin originates farther forward in the Bull Lake fish than in those from Keweenaw Bay, but the difference is slight, is subject to considerable overlap, and perhaps has no real significance.

In view of the notable differences in subsequent growth rate between stocks from Bull Lake and Keweenaw Bay (Fig. 4) there exists a strong possibility that early development, too, may differ in the same direction. If so, we may invoke a mechanistic explanation for the observed differences in fin and body proportions (Martin, 1949). Variations in developmental temperature are reflected in mean rate of growth and in size at which growth inflections occur. These in turn are important in the determination of the relative size of body parts, such as head and fins. In experimental lots of rainbow trout larger fins were produced by raising the temperature during early development (Martin, 1949).

Fin-ray counts of *Coregonus coulteri* (Tables 3-4) show some geographic variation in number of dorsal, anal, and pectoral rays but reveal nothing significant in pelvic-ray number. In the dorsal fin the usual number is 11 or 12 rays. At several localities these counts are equally frequent, but in Lakes McDonald and Superior there are usually 11 rays whereas in Bull Lake the modal count is 12. No consistent geographic pattern is suggested. In the anal fin 12 and 13 rays are most frequent, usually 12 rays in Lake McDonald and 13 in Lake Superior. A pectoral count of 16 is most frequent in Bull and McDonald Lakes, Montana. Elsewhere in the Columbia River drainage, in Alaska, and in Lake Superior, the most common count is 15.

In this as in the other fins, variation in the number of rays seems explainable as the result of local genetic emphasis or environmental modification. In any event the differences are not great, and the counts in the several populations overlap broadly.

There is no consistent positive correlation among the scale counts recorded (Tables 5–6). Lateral-line counts are maximal in Alaska, especially in Lake Aleknagik, are rather uniformly intermediate in the Columbia River system, and are lowest in Lake Superior. In the absence of certain of these stocks one might be inclined to recommend systematic partition of the others. In view of the rather complete gradation with extensive overlap between populations, however, such division seems pointless. Most populations usually have from 34 to 36 body-circumference scales, but the average number is considerably lower in McDonald Lake and higher in the Kicking Horse River—both in the Columbia basin. The most frequent caudal-peduncle scale count is 18 at all localities except Lake Aleknagik and Lake Superior, where counts of 19 and 20 are usual. As with the other counts the variations seem not to warrant special emphasis.

In the pygmy whitefish the number and the length of gillrakers are obviously correlated. In Alaska, the Kicking Horse River, and Arrow Lake the rakers are few (usually 13 to 16) and short (Table 7). Only one specimen was measured (Table 2), but the stubbiness of the rakers was noted during counting. In Diamond, Bull, McDonald, and Superior lakes the rakers typically number 16 to 19, and are notably longer (Table 2). Although there is overlap in numbers and probably in length, the differences in gillrakers are more marked than those in other characters. In view of the geographic implications, with some Columbia basin populations like the Lake Superior fish and others similar to Alaskan stocks, it seems improbable that each of the two structural types has a separate, monophyletic ancestry.

The acquisition by a lacustrine whitefish, even if it is a benthic form, of more and longer gillrakers is probably of adaptive advantage in obtaining food. It may be noted that the populations with the better developed and more numerous gillrakers are lacustrine. Three of the stocks with fewer rakers are from rivers or lakes dominated by rivers. If we assume that the species was chiefly a stream fish originally, it seems probable that relatively rapid parallel modification in two or more lakes has produced an increased length and number of gillrakers.

Comparisons with other species.—*Coregonus coulteri* was regarded by Evermann and Smith (1896) as the most distinctive of the North American members of the genus, a characterization which is still at least close to correct. Among the species of American coregonines, *coulteri* is the smallest, has the largest scales, the minimal number of gillrakers (13 to 20, about as in *cylindraceus*), the fewest vertebrae, and has only about one-fourth as many pyloric caeca as the lowest number reported among its congeners. The most obvious differences between the pygmy whitefish and the round whitefish, *C. cylindraceus,* are set forth in Table 8. Many of these same characters serve also to distinguish *coulteri* from the Rocky

TABLE 8.—*Comparison of the two species of the subgenus* Prosopium *in the Great Lakes area*

[Proportional measurements, calculated arithmetically, are based on 10 specimens of *Coregonus coulteri*, 74 to 107 millimeters in standard length, from Keweenaw Bay, and 10 individuals of *C. cylindraceus*, 236 to 377 millimeters long, from Lake Superior (Koelz, 1929: p. 632). Data for *C. cylindraceus* that are taken wholly or in part from Koelz (1929) are indicated by asterisks]

Character	*Coregonus coulteri*	*Coregonus cylindraceus*
Scales along lateral line	(55) 56-66 (70)	[1](80) 83-96 (100)*
Scales around body	(31) 33-37 (40)	(40) 42-46 (47)*
Scales around caudal peduncle	(16) 18-20	22-24
Size of exposed field of anterior lateral-line scales	Subequal to adjacent scales	Notably smaller than adjacent scales (scarcely smaller in small juveniles)
Vertebrae	52-54	59-63*
Pyloric caeca	15-23	87-117*
Pelvic fin rays	9-10 (11)	(10) 11 (12)
Dorsal fin rays	(10) 11-13 (14)	(13) 14-15
Upper jaw length in head length	3.1 to 3.4	3.9 to 4.8*
Mandible length in head length	2.3 to 2.6	2.7 to 3.1*
Gillraker length in head length	11.4 to 15.4	19.6 to 27.2*
Pelvic fin length in distance from pelvic insertion to anal origin	1.3 to 1.7	1.7 to 2.5*
Size	Small; maximum total length 149 millimeters (Lake Superior) to *ca.* 198 millimeters (Alaska)	Large; maximum weight about 5 pounds*

[1] Koelz (1929, p. 562) recorded a Lake Superior specimen of *cylindraceus* with 74 scales, 10 fewer than his next lowest count from the lake. It is conceivable that this was a hybrid with *coulteri*

Mountain whitefish, *C. williamsoni.* That species has longer and more numerous gillrakers, numbering 20 to 25, than do *coulteri* and *cylindraceus.*

DISTRIBUTION AND ABUNDANCE

General distribution.—The known range of the pygmy whitefish is confined to Lake Superior and certain waters on the Pacific slope from the headwaters of the Columbia River to south-central Alaska (Fig. 2). The species has not been collected in the Great Lakes other than Lake Superior. Trawling by the *Cisco* in northern and western Lake Huron in September and October 1952, was too limited to preclude the possibility of its occurrence there. It was not collected in much more extensive trawling in Green Bay, Lake Michigan, May 29–October 26, 1952, in southern Lake Michigan May 8, 1954–March 10, 1955, and in northern Lake Michigan May 14–September 7, 1955. The pygmy whitefish apparently either does not occur or is rare in these waters.

It may be anticipated that future investigation will yield additional records of the pygmy whitefish in the cold streams and deep lakes of the Pacific drainage from the Columbia River system to south-central Alaska. There is as yet no evidence of the existence of the species in the Mackenzie River basin, but it may possibly occur in deep lakes there as it does in Lake Superior. That the pygmy whitefish exists in northern United States or southern Canada, between Lake Superior and the Columbia River drain-

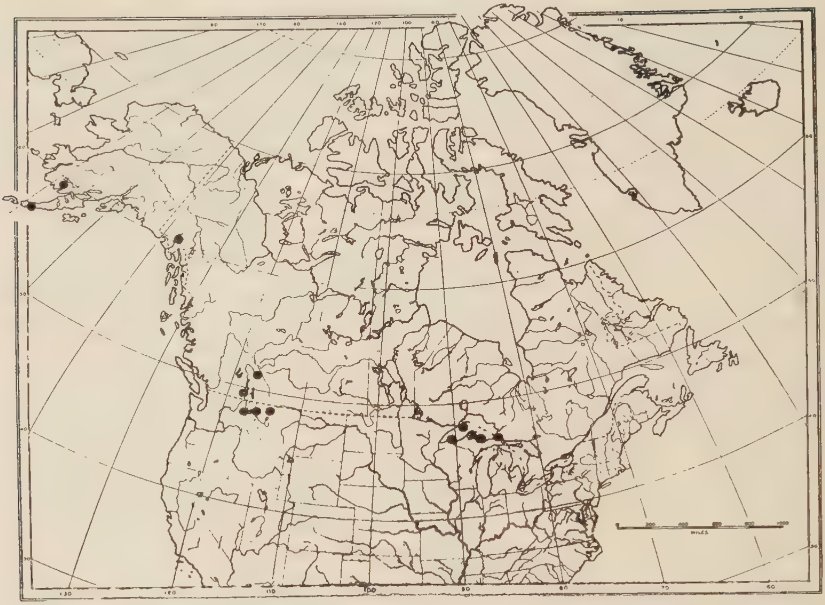

FIGURE 2.—Northern North America, showing collection localities for the pygmy whitefish.

age, however, seems unlikely. This region has been fairly well investigated and has few if any waters suitable to the species.

It is probable that *Coregonus coulteri* was a common and continuously distributed species near the periphery of the ice in late Pleistocene time. The few relict populations known to persist occupy some of the coldest waters of the United States, western Canada, and Alaska. Thus the present disjunct distribution may be regarded as due to survival in suitable habitats following the retreat of the Wisconsin glaciation. The results of radiocarbon analyses have demonstrated the relative recency of the last glaciation (Hough, 1953; Zumberge and Potzer, 1955). Hence, the finding that widely separated stocks of the pygmy whitefish differ little morphologically has a rational historical explanation. If the isolation of stocks was temporally remote, substantial structural differentiation would be expected.

Distribution and abundance in Lake Superior.—In Lake Superior the pygmy whitefish is widely distributed. Collection localities range from the Apostle Islands east to Whitefish Bay (about 290 miles) and north to Isle Royale (Fig. 3, Table 1). The species unquestionably occurs elsewhere. Collecting was restricted to areas with a suitable bottom for trawling where commercial fishing gear was not in use. No trawling was attempted along the entire northern and most of the eastern shore of the lake.

Although relatively few pygmy whitefish have been collected in other waters, Lake Superior has yielded 1,623 specimens. Of these, 68 percent

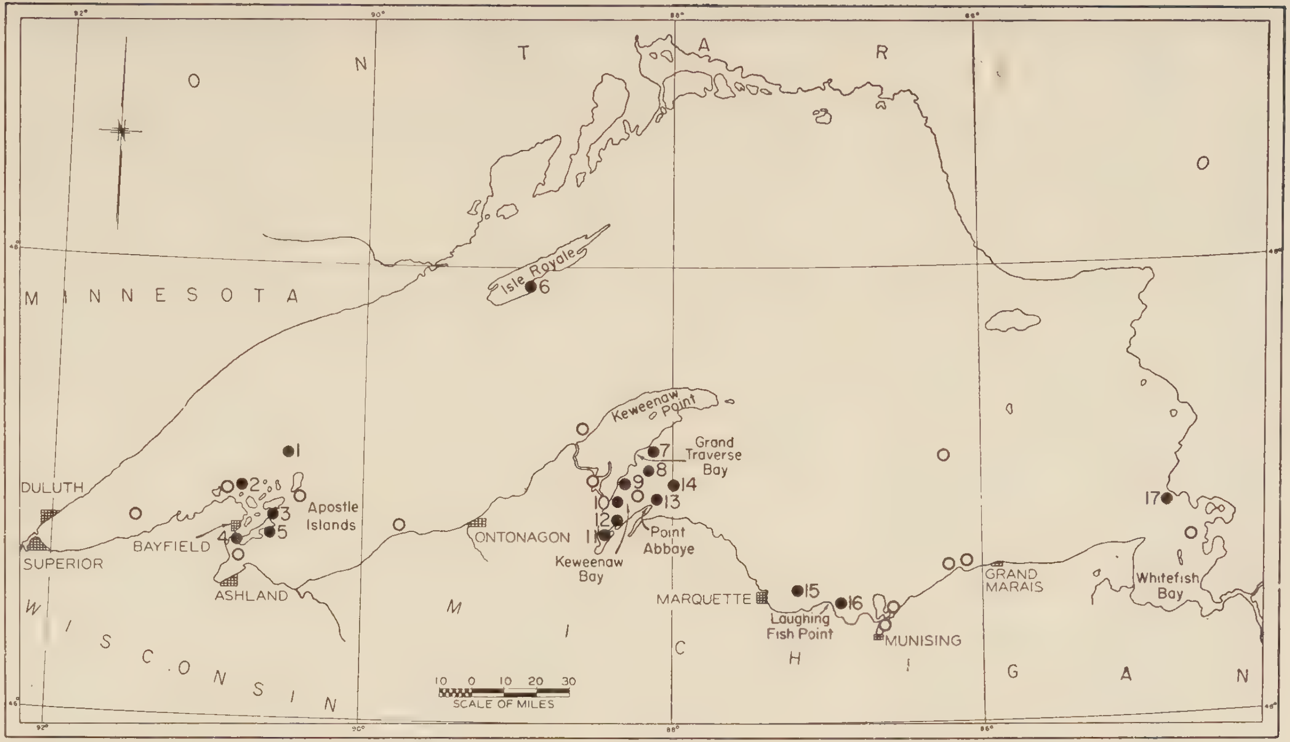
92°
90°
88°
86°
48°
46°
O N T A R I O
M I N N E S O T A
W I S C O N S I N
M I C H I G A N
Isle Royale
6
Keweenaw Point
Grand Traverse Bay
1
2
3
4
5
7
8
9
10
11
12
13
14
15
16
17
DULUTH
SUPERIOR
BAYFIELD
ASHLAND
Apostle Islands
ONTONAGON
Keweenaw Bay
Point Abbaye
MARQUETTE
Laughing Fish Point
MUNISING
GRAND MARAIS
Whitefish Bay
10 0 10 20 30
SCALE OF MILES

FIGURE 3.—Lake Superior, showing collecting stations (solid circles) for the pygmy whitefish and localities of special interest in this study. Open circles indicate trawling stations where the species was not taken.

were obtained in Keweenaw Bay (Fig. 3, Stations 9 to 12), 23 percent in Siskiwit Bay, Isle Royale (Station 6), 4 percent off Laughing Fish Point (Station 16), 2 percent in the Apostle Islands (Stations 1 to 5), and the remaining 3 percent at other localities. The number of fish taken at the several stations is not directly indicative of the abundance in these areas because of variation in fishing time. Nevertheless, the pygmy whitefish was more plentiful in Siskiwit Bay and in Keweenaw Bay than elsewhere. In Siskiwit Bay as many as 171 fish were collected in a single 10-minute haul (more than 80 percent were young of the year), and the average in the area was 52 per haul. In Keweenaw Bay (Stations 9 to 12) 85 were obtained from a single haul and the average catch in 74 drags was 15 fish. The maximum catch per haul did not exceed 15 at other stations, except for 20 fish taken in a 9-minute haul at Station 14. At two of the *Cisco's* major collection areas, the Apostle Islands and Laughing Fish Point, the average catch on dates when pygmy whitefish were taken was only 2 per haul.

Pygmy whitefish were not collected at 14 stations fished during 1953. The open circles of Figure 3 designate localities at which a minimum of 20 minutes of trawling failed to collect the species, even though the catch of other fish indicated that the trawl was operating satisfactorily. Trawling at 9 of these stations was at depths above, below, or near the limits of the known bathymetric distribution of *Coregonus coulteri* in Lake Superior. Comparison of localities of proper depth indicates that trawling was successful chiefly in a protected habitat. Three of the 5 unsuccessful stations of suitable depth are in exposed situations; 3 of the 4 major sampling areas (Siskiwit and Keweenaw Bays, Apostle Islands) are well protected, and the other (Laughing Fish Point) is partly protected from prevailing winds. In exception to this apparent preference for a protected habitat, the pygmy whitefish was not caught in Munising Bay, Munising, Michigan. Here about 2 hours of trawling on June 17–22 at depths of 15–39 fathoms failed to take pygmy whitefish, but the lake whitefish was far more abundant than at any other locality fished.

BATHYMETRIC DISTRIBUTION

The bathymetric range of the pygmy whitefish at Station 11 in southern Keweenaw Bay (Fig. 3), where 58 percent of our specimens were obtained, extended from 10 to 49 fathoms (Table 9). Although taken at all depths fished, it was most plentiful at 25–39 fathoms; the average maximum rate of capture (37 per 10-minute haul) was at the 30- to 34-fathom interval. The distribution was similar throughout the season, but on August 2 many fish were taken at 15–19 fathoms, and on May 11 the only fish caught were at 45–49 fathoms. This latter collection indicated a distribution similar to that at Laughing Fish Point (Station 16) early in 1954. There, on January 11, 40 minutes of trawling at 43–54 fathoms yielded 5 pygmy whitefish, whereas 30 minutes of fishing at the same station on January 7 at 26–40

TABLE 9. — *Numbers of pygmy whitefish captured per 10-minute drag of an otter trawl in southern Keweenaw Bay (Station 11), Lake Superior, 1953*

[Number of minutes of trawling in parentheses]

Depth[1] (fathoms)	May 11	July 11	August 2	September 11	October 2-3	October 15	Average
10-14	...	...	0.5 (20)	0.0 (10)	...	3.0 (10)	1.0 (40)
15-19	...	...	22.0 (20)	4.0 (10)	0.0 (10)	...	12.0 (40)
20-24	...	...	...	2.0 (10)	14.5 (20)	1.5 (20)	6.8 (50)
25-29	...	0.0 (10)	19.7 (30)	24.9 (35)	...	23.3 (75)	21.4 (150)
30-34	...	41.5 (20)	19.2 (40)	54.4 (39)	32.3 (13)	...	37.0 (112)
35-39	0.0 (6)	...	7.0 (10)	...	...	51.0 (10)	22.3 (26)
40-44	0.0 (58)	...	...	40.0 (10)	...	10.0 (20)	6.8 (88)
45-49	0.6 (65)	...	...	...	...	...	0.6 (65)

[1] Placement of individual hauls based on the mean of the shallowest and deepest water fished. Most tows paralleled isobaths in water of nearly constant depth

fathoms failed to take the species. Perhaps pygmy whitefish are confined to waters of considerable depth during the winter and spring.

The average length of pygmy whitefish increased directly with water depth in southern Keweenaw Bay in 1953 (Table 10). Mean total lengths in the combined collections ranged from 71 millimeters (2.8 inches) at 10–19 fathoms to 116 millimeters (4.6 inches) at 40–49 fathoms. (The trend was similar in individual collections.) This relationship was caused by differences in the depth distribution of age groups. All fish collected at the shallowest interval (10–14 fathoms) were yearlings; the percentage of fish of this age declined with increase in depth to 7 percent at 40–44 fathoms and nil at 45–49 fathoms.

Some seasonal change occurred in the bathymetric distribution of I-group pygmy whitefish. At depths greater than 29 fathoms, the percentage of I-group fish taken within a specific 5-fathom depth interval increased somewhat with the progress of the season. At the 30- to 34-fathom interval, for example, yearlings made up only 16 percent and 14 percent of the catch on July 11 and August 2, but accounted for 32 percent on September 11 and 65 percent on October 2–3. At 35–39 fathoms the percentage of I-group whitefish was nil on August 2 and 16 on October 15; at 40–44 fathoms it was 5 on September 11, and 11 on October 15. These increases

TABLE 10.—*Average total length (millimeters) of pygmy whitefish caught at different depths in southern Keweenaw Bay (Station 11) Lake Superior, 1953*

[Number of fish in parentheses. Data presented are from preserved fish; 83 were discarded]

Depth (fathoms)	May 11[1] July 11	August 2	September 11	October 2-3	October 15	Average	Percentage of yearlings in catch
10-14	...	69 (1)	...	...	80 (3)	77 (4)	100
15-19	...	70 (39)	76 (2)	...	...	70 (41)	95
20-24	...	...	...	84 (22)	78 (3)	83 (25)	72
25-29	...	103 (59)	[2]87 (105)	...	94 (171)	93 (335)	49
30-34	102 (81)	105 (28)	99 (192)	89 (34)	...	99 (335)	30
35-39	...	116 (7)	...	...	104 (50)	105 (57)	14
40-44	...	...	118 (40)	...	113 (19)	116 (59)	7
45-49	116 (4)	...	...	...	...	116 (4)	0

[1] The collection at 30-34 fathoms was made July 11; that at 45-49 fathoms on May 11

[2] Includes 17 fish collected at 30 fathoms and 2 fish from 21 fathoms

in percentage of I-group fish are reflected in the mean lengths of Table 10. Yearlings collected at different depths on the same date showed no significant difference in average length.

The rate of capture of pygmy whitefish on September 7 in Siskiwit Bay (Station 6) was slightly higher at 15–19 and 20–24 fathoms (23 and 24 fish per haul) than at 35–39 fathoms (17 fish per haul). On September 30 more fish were taken in a haul at 10–14 fathoms (171) than at 15–19 fathoms (95), the only depths fished. Most were 0- or I-group fish. Data for collections at other stations in Lake Superior were too scanty for analysis but indicated a vertical distribution according to size and age similar to that in Keweenaw Bay.

AGE AND GROWTH

Age was determined for 271 pygmy whitefish collected in Keweenaw Bay (Station 11) on October 2 and 15, 1953, 94 caught in Siskiwit Bay (Station 6) on September 7, 32 taken in the Apostle Island region (Stations 2–5) on May 30–July 30, and 37 from Laughing Fish Point (Station 16), July 13, 1953–January 11, 1954. Scales were mounted in a glycerin-gelatin medium and diameters within annuli were measured at the magnification × 84. Growth calculations were by direct proportion.

Keweenaw Bay.—Calculated total lengths at the end of each year of life for 123 male and 148 female pygmy whitefish from Keweenaw Bay (Table 11) reveal extraordinarily slow growth. The two oldest fish, both nearing the end of their eighth growing season, were only 5.4 inches long at the time of collection.

TABLE 11. — *Average calculated total length (millimeters) and length at capture of pygmy whitefish collected in Keweenaw Bay, October 2 and 15, 1953*

Age group	Sex	Number of fish	Total length at capture		Weight (grams)	Calculated length at end of year of life						
			Inches	Millimeters		1	2	3	4	5	6	7
I	Male	61	3.0	76	2.3	54	..	..	...	...	...	...
	Female	57	3.0	77	2.4	55	..	..	...	...	...	...
II	Male	14	3.7	94	4.7	42	76	.	...	...	...	...
	Female	15	4.0	101	6.1	36	76	..	...	...	...	...
III	Male	5	4.0	102	5.9	42	75	95	...	...	...	...
	Female	10	4.2	106	7.5	40	75	92	...	...	...	...
IV	Male	25	4.2	106	7.8	44	69	87	99	...	...	...
	Female	26	4.7	120	12.9	42	69	91	111	...	...	...
V	Male	18	4.3	110	8.8	44	70	86	97	106	...	...
	Female	35	5.0	126	15.2	41	65	86	104	118	...	...
VI	Female	3	5.0	128	16.1	46	68	90	105	115	123	...
VII	Female	2	5.4	136	20.4	37	60	79	95	110	122	130
Average increment	Male	123	...	...	....	49	28	17	12	9	...	...
	Female	148	...	...	....	46	29	21	19	14	10	8
Average length	Male	123	...	...	....	49	71	87	98	106	...	...
	Female	148	...	...	....	46	69	88	107	117	123	130
Increment of average	Male	123	...	...	....	49	22	16	11	8	...	...
	Female	148	...	...	....	46	23	19	19	10	6	7

Female pygmy whitefish consistently averaged longer and heavier at capture than did males of the same age. The difference in length ranged from 1 millimeter (I group) to 16 millimeters (V group); the weight advantage of the females varied from 0.1 gram (I group) to 6.4 grams (V group). In age-group V, females were 73 percent heavier than males. The annual increments of length indicate a first-year advantage for males (49 millimeters as compared with 46 millimeters for females), nearly equal growth in the second year (28 and 29 millimeters), and more rapid growth for females in the next 3 years. The calculated lengths for the age-groups exhibit some indication of "Lee's phenomenon." Except for the first-year length of age-group I the trend is not sharp, but it is sufficient to produce discrepancies between average increments and increments of the average (Table 11). Comparison of lengths at collection and calculated lengths of fish of the various age groups indicates that the growing season may have been nearly completed by the date of collection.

Despite irregularities in the data, the percentage of males decreased with age. Males made up 51 percent of the fish in age-groups I and II, 45 percent of those in age-groups III and IV, and only 31 percent of age-groups V-VII (only females in VI and VII groups). This trend is reflected in the average age (number of annuli) which was 2.4 for males and 2.9 for females. The complete sample was 45 percent male.

The poor numerical representation of age-groups II and III (in comparison with age-groups I, IV, and V) suggests that year-classes 1950 and 1951 may have been relatively weak. Wide fluctuations in the strength of year classes have been observed frequently in Great Lakes fishes (including coregonines). The small numbers of whitefish in age-groups VI and VII may result from normal mortality rather than weakness of year classes.

With the exception of age-groups I and II, the length-frequency distribution at the time of collection of adjacent age groups of pygmy whitefish in Keweenaw Bay exhibited extensive overlap (Table 12). Length alone, therefore, can be employed with confidence for the identification of all but the largest fish (3.4-3.5 inches) in the I-group but at greater age is undependable. Every length interval beginning with 3.8-3.9 inches included members of 2 to 4 age groups.

TABLE 12. — *Length-frequency distribution of age groups of pygmy whitefish collected in Keweenaw Bay, October 2 and 15, 1953*

[M = male; F = female]

Total length		I		II		III		IV		V		VI	VII	Total		
Inches	Millimeters	M	F	M	F	M	F	M	F	M	F	F	F	M	F	Both sexes
2.2-2.3	55- 59	..	1	..	..	..	..	..	..	..	..	..	..	..	1	1
2.4-2.5	60- 64	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
2.6-2.7	65- 69	5	3	..	..	..	..	..	..	..	..	..	..	5	3	8
2.8-2.9	70- 74	19	15	..	..	..	..	..	..	..	..	..	..	19	15	34
3.0-3.1	75- 80	27	22	..	..	..	..	..	..	..	..	..	..	27	22	49
3.2-3.3	81- 85	8	13	..	..	..	..	..	..	..	..	..	..	8	13	21
3.4-3.5	86- 90	2	3	3	..	..	..	..	..	..	..	..	..	5	3	8
3.6-3.7	91- 95	..	..	5	2	..	..	..	..	..	..	..	..	5	2	7
3.8-3.9	96-100	..	..	5	5	2	3	5	..	..	..	..	..	12	8	20
4.0-4.1	101-105	..	..	1	6	1	1	7	..	5	..	..	..	14	7	21
4.2-4.3	106-110	..	..	..	2	2	2	11	..	3	..	..	..	16	4	20
4.4-4.5	111-115	..	..	..	..	..	4	2	5	9	1	..	..	11	10	21
4.6-4.7	116-120	..	..	..	..	..	..	..	10	1	2	..	..	1	12	13
4.8-4.9	121-125	..	..	..	..	..	..	..	7	..	14	1	..	..	22	22
5.0-5.1	126-130	..	..	..	..	..	..	..	3	..	13	1	..	..	17	17
5.2-5.3	131-135	..	..	..	..	..	..	..	1	..	4	1	1	..	7	7
5.4-5.5	136-140	..	..	..	..	..	..	..	..	..	1	..	1	..	2	2
Total....................		61	57	14	15	5	10	25	·26	18	35	3	2	123	148	271

Siskiwit Bay, Isle Royale.—The growth rate of pygmy whitefish was even slower in Siskiwit Bay (Table 13) than in Keweenaw Bay. With the exception of the second year of life all calculated annual increments of length were greater in Keweenaw Bay than in Siskiwit Bay. The maximum difference in rate was in the fourth year of life of females (11 millimeters in Siskiwit Bay; 19 millimeters in Keweenaw Bay). Despite the more rapid growth in Keweenaw Bay, the data for the two stocks exhibit certain similarities. In both areas, for example, females were larger than males at capture (exception in I-group of Siskiwit Bay). Sex differences of calculated growth also were similar. Males had the higher first-year increments, the growth of the sexes was nearly equal in the second year, and females had the greater increments in later years of life.

TABLE 13. — *Average calculated total length (millimeters) and length at capture of pygmy whitefish collected in Siskiwit Bay, Isle Royale, September 7, 1953*

Age group	Sex	Number of fish	Total length at capture[1]		Calculated length at end of year of life			
			Inches	Millimeters	1	2	3	4
O	Unknown......	12	1.4	36	..	..	..	..
I	Male..........	17	2.5	63	42	..	..	..
	Female........	10	2.3	59	41	..	..	..
II	Male..........	22	3.1	78	38	68	..	..
	Female........	5	3.2	81	37	67	..	..
III	Male..........	18	3.3	85	39	68	81	..
	Female........	11	3.5	88	32	62	80	..
IV	Male..........	1	3.6	92	46	72	81	88
	Female........	10	3.9	100	39	65	85	96
Average increment	Male..........	58	...	...	40	29	13	7
	Female........	36	...	...	37	28	19	11
Average length	Male..........	..	...	...	40	68	81	88
	Female........	..	...	...	37	64	82	96
Increment of average	Male..........	..	...	...	40	28	13	7
	Female........	..	...	...	37	27	18	14

[1] These fish were not weighed because they had been transferred from formalin to alcohol after collection

The sex ratio of Siskiwit Bay fish varied erratically among the age groups, but the oldest (IV) was strongly dominated by females. The numerical abundance of the age groups gives no indication of weakness in the 1950 and 1951 year classes, both of which were poorly represented in Keweenaw Bay.

The Apostle Islands.—The limited collection of pygmy whitefish from the Apostle Islands shows that growth was more rapid in this region than in Siskiwit or Keweenaw Bay. The average calculated total lengths in millimeters at the end of each year of life[3] for 32 fish collected May 30–July 30, 1953, are shown below (number of fish in parentheses):

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[3] All age groups were combined. Because of difficulty in determining whether a new annulus had formed on scales of some fish collected May 30, only average lengths computed from scale measurements within visible annuli are included in the table.

	Calculated length at end of year of life						
	1	2	3	4	5	6	7
Trawl collection							
Males	50	75	95	108	......	......	......
	(6)	(5)	(5)	(2)	......	......	......
Females	46	72	94	112	122	126	136
	(21)	(21)	(20)	(16)	(9)	(4)	(3)
Gill-net collection							
Females	44	68	98	117	129	139	144
	(5)	(5)	(5)	(5)	(5)	(5)	(2)

The growth pattern for the sexes was similar to that described for Siskiwit and Keweenaw Bays. The average length of fish from trawl collections in the Apostle Islands was greater than that of fish from Keweenaw Bay (Table 11) for both sexes and at all ages, with the single exception of females at the end of the first year. Differences in rate of growth in these two regions were of about the same magnitude as differences in rate of growth between Keweenaw and Siskiwit Bays.

The single gill-net collection of pygmy whitefish is shown separately from trawl collections because the gill nets (1-inch mesh, extension measure) were obviously selective for fast-growing fish of large size. That this species attains a larger size in the Apostle Islands than elsewhere in Lake Superior is suggested by its capture in gill nets in this area only although other localities were fished with identical gear. Whereas 900 feet of 1-inch-mesh gill net captured 6 fish at this station, 27,600 feet of net set within the known bathymetric range of the species at other localities failed to take it. A total of 8,400 feet of this net was set in the Keweenaw Bay region, where the species was known to be abundant.

Laughing Fish Point.—The collection of pygmy whitefish from Laughing Fish Point for which ages were determined was limited to 25 fish of the I-group, and only 12 of other age groups. Despite minor discrepancies, presumably because of the small sample, a growth rate similar to that in Keweenaw Bay is indicated. A summary of the data for fish of age groups I to VI follows (number of fish in parentheses):

	Calculated length at end of year of life					
	1	2	3	4	5	6
Males	48	79	92	102	106	......
	(22)	(6)	(3)	(3)	(1)	......
Females	46	68	90	106	118	123
	(15)	(6)	(5)	(4)	(2)	(1)

As in the other regions calculated length of females was less than that of males for the first two years, about equal during the third, and exceeded that of males for the fourth and later years of life.

Length of young of the year.—Collections of young-of-the-year pygmy whitefish in Lake Superior indicated that fish of this age were showing good growth during September and October (Table 14). Although the numbers of fish collected were usually small, their average lengths showed a progressive increase from 36 and 35 millimeters on September 7 and 10, to 45 and 49 millimeters on October 5 and 21.

Growth in Bull and McDonald Lakes, Montana.—That growth rate of pygmy whitefish was faster in Bull and McDonald Lakes, Montana, than in Lake Superior is shown by the curves of Figure 4, which compare calculated lengths at the end of each year of life for fish from these waters and from Keweenaw and Siskiwit Bays. Data for fish from the Montana waters are as follows (number of fish in parentheses):

TABLE 14. — *Length of O-group pygmy whitefish in Lake Superior, 1953*

Collection locality[1]	Date	Number of fish	Total length (millimeters)	
			Range	Average
Keweenaw Bay (9)	Sept. 5	1	....	31
Siskiwit Bay (6)	Sept. 7	12	32-40	36
Point Abbaye (13)	Sept. 10	5	31-39	35
Laughing Fish Point (16)	Sept. 14	13	33-39	37
Siskiwit Bay (6)	Sept. 30	137	35-49	42
Laughing Fish Point (16)	Oct. 5	9	40-54	45
do	Oct. 21	3	47-51	49

[1] Station numbers (Fig. 3) are in parentheses

Lake McDonald	*Calculated length at end of year of life*[4]			
	1	*2*	*3*	*4*
Males	64	88	101	108
	(26)	(26)	(23)	(2)
Females	62	92	108	......
	(6)	(6)	(6)	......
Bull Lake				
Males	59	113	130	......
	(20)	(20)	(10)	......
Females	60	119	152	......
	(2)	(2)	(2)	......

At the age of 3 years, the average length of male pygmy whitefish from Bull Lake was 60 percent greater than in Siskiwit Bay; for females this percentage was 85. The increment during the second year of life, which showed the widest deviation, was nearly double that of Lake Superior fish. Almost no change in growth rate was shown by the fish from Bull Lake during the first 2 years of life, whereas this rate declined about 40 percent during the second year in Keweenaw Bay. An even sharper decline (about

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[4] Since the dates of collection were December 26 and January 12 (Bull Lake) and November 17 (Lake McDonald), an annulus at the periphery of the scales was assumed and length at collection was considered equivalent to calculated length.

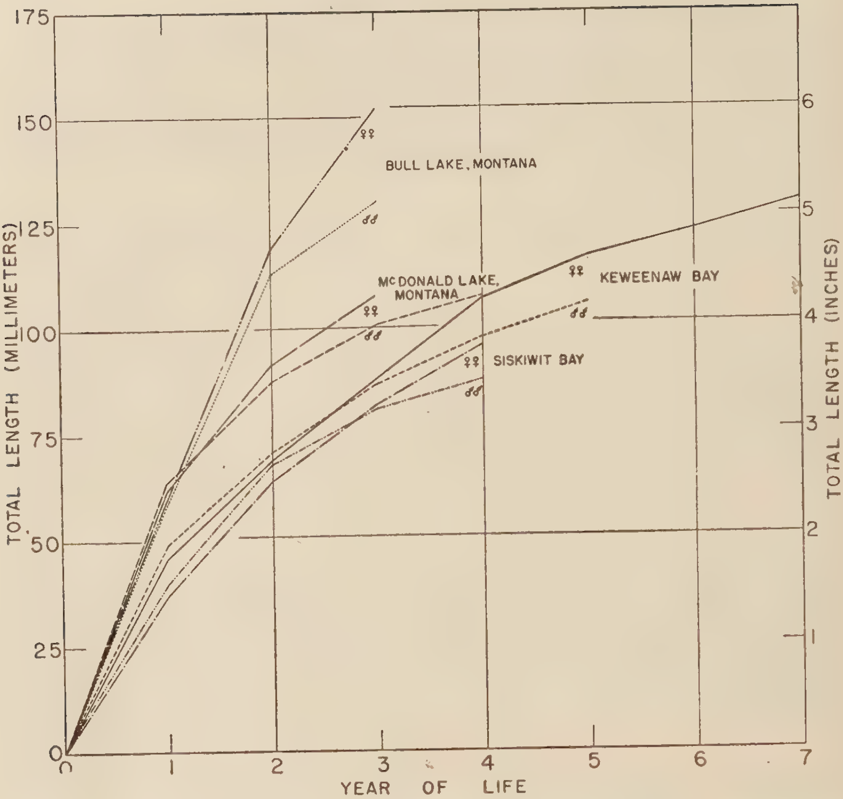

FIGURE 4.—Calculated growth in length of pygmy whitefish from Bull and McDonald Lakes, Montana, and Keweenaw and Siskiwit Bays, Lake Superior.

55 percent) in growth rate during the second year was indicated by pygmy whitefish of the Lake McDonald collection. Although these fish attained a first-year calculated length slightly greater than that of fish from Bull Lake, their growth curves during subsequent years were roughly parallel with those of fish from Lake Superior.

LENGTH-FREQUENCY DISTRIBUTION

The length-frequency distribution of 1,521 pygmy whitefish collected in Lake Superior in 1952–1954 (Table 15) is given separately for the four principal areas of capture. Collections from Keweenaw Bay and vicinity are tabulated in part according to sex and date.

The total length of pygmy whitefish taken by trawling in Lake Superior ranged from 1.2 to 5.7 inches. Only the young of the year and yearlings stood out reasonably well in the length-frequency distribution. The O group

TABLE 15. — *Length-frequency distribution of pygmy whitefish collected by trawling in Lake Superior, 1952-1954*
[M = male; F = female]

Total length (inches)	Keweenaw Bay and vicinity (Stations 7 to 14)									Siskiwit Bay (Station 6) Sept. 7-30, 1953	Laughing Fish Point (Station 16) July 13, 1953-Jan. 11, 1954	Apostle Islands (Stations 1-5) Aug. 20, 1952 and May 30-July 30, 1953	All fish[2]
	May 7-July 11, 1953		Aug. 2, 1953		Sept. 5-11, 1953		Oct. 2-15, 1953		Total[1]				
	M	F	M	F	M	F	M	F					
1.2-1.3......	...	...	...	...	...	...	...	...	3	5	2	...	10
1.4-1.5......	...	...	...	...	...	...	...	...	3	23	11	...	37
1.6-1.7......	...	...	...	...	...	...	...	...	...	96	6	...	102
1.8-1.9......	...	...	...	...	...	...	...	...	...	25	3	...	28
2.0-2.1......	...	1	...	...	...	...	...	...	1	2	3	...	6
2.2-2.3......	...	...	...	...	...	...	...	1	1	4	...	...	5
2.4-2.5......	6	...	1	5	1	1	...	...	17	27	3	...	47
2.6-2.7......	9	10	13	11	...	17	8	5	88	62	1	...	151
2.8-2.9......	19	9	9	6	30	18	21	23	164	46	5	1	216
3.0-3.1......	1	...	5	1	38	21	40	33	153	28	14	...	195
3.2-3.3......	1	...	1	...	5	1	14	17	40	14	5	...	60
3.4-3.5......	3	4	1	2	2	1	4	3	22	23	...	...	47
3.6-3.7......	7	3	6	2	10	4	6	3	45	7	3	2	57
3.8-3.9......	7	7	11	3	16	9	13	8	86	5	1	1	93
4.0-4.1......	6	3	6	2	27	7	14	7	77	4	...	2	83
4.2-4.3......	8	2	3	4	18	6	17	4	64	1	2	1	68
4.4-4.5......	1	4	2	9	10	12	11	10	62	...	2	3	67
4.6-4.7......	...	11	...	10	3	21	1	13	64	...	2	6	72
4.8-4.9......	...	9	...	13	...	32	...	22	79	...	1	3	83
5.0-5.1......	...	5	...	6	...	18	...	17	47	...	1	3	52
5.2-5.3......	...	4	...	2	...	10	...	7	25	...	...	4	29
5.4-5.5......	...	1	...	...	...	2	...	2	8	...	...	3	11
5.6-5.7......	...	...	...	...	...	1	...	...	1	...	...	1	2
Total.......	68	73	58	76	160	181	149	175	1,050	372	65	30	1,521
Average length......	3.3	4.0	3.4	4.0	3.6	4.1	3.5	3.9	3.7	2.4	2.7	4.7	3.4

[1] Includes 110 fish for which sex is not given. Of these, 20 were caught August 16, 1952

[2] Includes 1 fish from Station 15 and 3 from Station 17 not shown elsewhere in table. Of 1,623 pygmy whitefish collected, 102 were not measured

was well separated from the I group in the Keweenaw Bay and Laughing Fish Point regions, but in the slowly growing population of Siskiwit Bay it tended to overlap the I group slightly by September 30 (all fish less than 2.0 inches long were of the O group). In Keweenaw Bay age-group I was reasonably distinct from older age groups in the collections of May 7 to August 2 (all fish less than 3.2 inches), and September 5-11 (less than 3.4 inches), but by October the largest of the yearlings had overtaken the smallest fish of the II group. Probably the demarcation of the I group would have been even less distinct if age-groups II and III had been represented by strong year classes; both were rather poorly represented in 1953. In Siskiwit Bay, where age-groups II and III were well represented, the length-frequency distribution of age-group I overlapped broadly those of older age groups.

Separation of males from females in the length-frequency distribution for pygmy whitefish from Keweenaw Bay emphasizes the sexual differences in growth rate and life span (p. 181). All fish longer than 4.7 inches were females (Table 15), except for a 5.0-inch male (age-group VI) collected at Station 15 on August 12, 1953.

The mean length of pygmy whitefish caught by trawling in Lake Superior was 3.4 inches. The length averaged 2.4 to 4.7 inches at the major collecting areas. The smallest average lengths (2.4 and 2.7 inches) were at Siskiwit Bay and Laughing Fish Point, where 38 to 40 percent of the fish caught were young of the year, and where few large fish were taken. In the Apostle Islands region, in contrast, few young fish were collected; the average length was 4.7 inches.

REPRODUCTION

Age and size at maturity.—All male pygmy whitefish of age-group II or older in collections from Keweenaw Bay, October 2–15, 1953, and from Siskiwit Bay, Isle Royale, September 7, were sexually mature (Table 16). A few I-group males (7 percent) from Keweenaw Bay also were mature.

Relatively few II-group females were mature (3 of 15 in Keweenaw Bay on October 2–15, none of 5 in Siskiwit Bay on September 7, and 3 of 11 on September 30 [5]). Of the III-group females, 6 of 10 from Keweenaw Bay and 8 of 11 from Siskiwit Bay were mature and all fish of older age groups were mature in both collections. The age at which 50 percent or more of the pygmy whitefish were mature in Lake Superior was 2 years for males and 3 years for females.

In Weisel and Dillon's (1954) collections from Bull Lake, Montana, all I-group pygmy whitefish were sexually mature. These fish were much larger than the Lake Superior fish, however (p. 185), and were apparently taken from a spawning aggregation, in which immature fish would not be expected. Mature yearling males also occurred in fish from a spawning

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[5] These 11 fish were part of a large collection in which all but 12 were members of age-group I (the twelfth fish belonged to the III-group). Ages were determined by the examination of scales, but no scale measurments were made

TABLE 16. — *Age at attainment of maturity in pygmy whitefish, Lake Superior, 1953*

Age group	Keweenaw Bay, October 2-15				Isle Royale, September 7				Percentage mature, all fish	
	Males		Females		Males		Females			
	Number of fish	Percentage mature	Number of fish	Percentage mature	Number of fish	Percentage mature	Number of fish	Percentage mature	Males	Females
I........	61	7	57	0	17	0	10	0	5	0
II.......	14	100	15	20	22	100	5	0	100	15
III......	5	100	10	60	18	100	11	73	100	67
IV-VII...	43	100	66	100	1	100	10	100	100	100

aggregation collected in Lake McDonald, Montana, November 17, 1936.

The data on length at which pygmy whitefish attain sexual maturity (Table 17) are based on 799 fish collected in Keweenaw Bay between August 2 and October 15, 1953, after seasonal development of the gonads had progressed sufficiently to permit accurate determination of maturity. Some males were mature at a total length of 3.0–3.1 inches and some females at 3.8–3.9 inches. Percentage maturity increased progressively with increasing length. Fifty percent or more of the fish were mature at the 3.4- to 3.5-inch class in males and at the 4.2- to 4.3-inch interval for females. All larger fish of each sex were mature.

TABLE 17.—*Length at attainment of maturity in pygmy whitefish, Keweenaw Bay, Lake Superior*

[Stations 9, 11, and 13, August 2-October 15, 1953]

Total length (inches)	Males		Females	
	Number of fish	Percentage mature	Number of fish	Percentage mature
2.2-2.9	83	0	87	0
3.0-3.1	83	7	55	0
3.2-3.3	20	25	18	0
3.4-3.5	7	71	6	0
3.6-3.7	22	100	9	0
3.8-3.9	40	100	20	10
4.0-4.1	47	100	16	31
4.2-4.3	38	100	14	86
4.4-5.7	27	100	207	100

Sex ratio.—Treatment of the sex ratio of different age groups (p. 182) brought out a somewhat erratic variability[6] but demonstrated an unmistakable trend for males to be scarce or lacking in the older age groups, thus providing an explanation for the predominance of females in most collections. The scarcity of older males in combination with their relatively slow growth led to an unusual relationship between sex ratio and length of pygmy whitefish in Keweenaw Bay in 1953. A summary of data tabulated according to length and sex in Table 15 yields the following:

Total length (inches)	*Number of fish*	*Percentage males*
2.0–3.5	422	55
3.6–3.9	115	66
4.0–4.3	134	74
4.4–4.5	59	41
4.6–4.7	59	7
4.8–5.7	151	0

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[6] The unreliability of sex ratios shown by small numbers of fish was emphasized by collections in Siskiwit Bay. In this area 22 of 27 II-group fish collected September 7 were males, but all of 11 II-group fish collected on September 30 at this station were females. This apparent segregation of the sexes probably was not typical, as it was not observed in other collections.

Males were only slightly more numerous than females at 2.0-3.5 inches, reached a predominant position at 4.0–4.3 inches, and dwindled rapidly at 4.6–4.7 inches, the largest length interval in which they were represented at all.

Fecundity.—Maturing eggs were counted in the ovaries of 63 pygmy whitefish collected in Lake Superior in 1953. Egg production ranged from 93 to 597 and averaged 362 (Table 18). The average number of eggs produced by fish of each ½-inch length group rose from 121 at 3.4–3.9 inches to 531 at 5.5-5.9 inches. The mean production of eggs per gram of weight ranged between the narrow limits of 20 and 31 and averaged 26 or 27 for all length groups.

TABLE 18. — *Production of eggs by pygmy whitefish in Lake Superior, 1953*

[Collection localities and dates were as follows: 57 fish from Keweenaw Bay (Station 11), September 11-October 15; 3 (the smallest in the series, 87-91 millimeters) from Siskiwit Bay (Station 6), September 30; 1 (the largest fish, 149 millimeters) from the Apostle Islands (Station 3), July 29; and 2 (117 and 123 millimeters) off Laughing Fish Point (Station 16), October 21]

Total length (inches)	Average weight[1] (grams)	Number of fish	Number of eggs		Number of eggs per gram of fish[2]	
			Range	Average	Range	Average
3.4-3.9	5.9 (1)	4	93-156	121	.....	26
4.0-4.4	8.9 (8)	9	146-285	235	21-30	27
4.5-4.9	13.5 (22)	26	248-440	344	20-31	26
5.0-5.4	17.0 (17)	20	385-586	457	20-31	26
5.5-5.9	21.9 (2)	4	489-597	531	26-26	26

[1] Numbers of fish weighed (in parentheses) show basis of estimates of numbers of eggs per gram of fish

[2] Mean of values for individual fish

In the graphical presentation of egg production (Fig. 5), a line drawn by inspection through the points representing egg production of individual fish has a sigmoid form. The section of steepest rise, between the lengths of 4.3 and 4.7 inches, depicts an average increase of about 160 eggs per ½-inch increase of length. A decrease in rate to about 100 eggs per ½-inch of length is indicated by the section of the curve for fish of 5.4 to 5.9 inches. Although the values were rather uniformly distributed about the curve, figures for some individuals were scattered. The greatest deviation for fish of about equal size was shown by two fish (5.3 and 5.4 inches long) which had egg counts of 388 and 586, a difference of 51 percent.

The ovaries of a 117-millimeter female pygmy whitefish collected off Laughing Fish Point on October 21, 1953, contained 78 partly resorbed eggs which had apparently been retained from the previous spawning season. These eggs equalled 36 percent of the average production (Fig. 5) for a fish of its calculated length (108 millimeters) at the approximate time of its failure to expel all of its eggs. Since many eggs may have been resorbed before the time of collection, this fish may not have spawned at all during the previous year. The presence of the partly resorbed eggs in

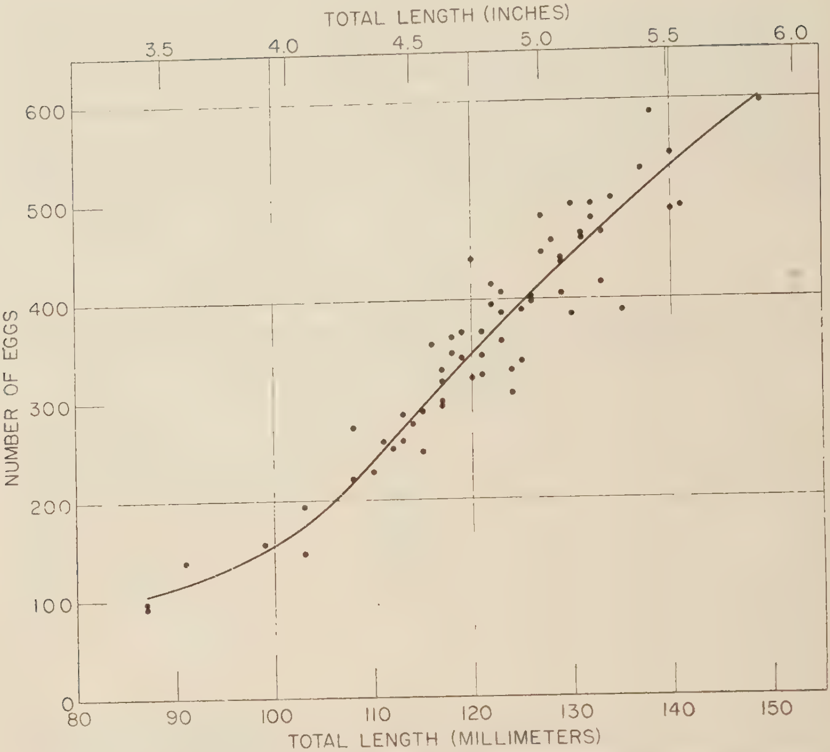

FIGURE 5.—Relationship of length of fish to number of eggs in ovaries of pygmy whitefish. The data are summarized in Table 18.

the ovary did not interfere with production because the 295 new eggs in its ovaries were only 6 percent below the average number for three other fish of the same length.

Residual mature eggs were rarely seen in other ovaries, although one spent female collected January 11, 1954, had 15 such eggs and another had 1.

Time and locality of spawning.—Although no collections of pygmy whitefish were made during the breeding season, spawning in the Laughing Fish Point region undoubtedly occurred during November or December 1953. Ovaries of 2 females of the last fall collection (October 21) were not yet ripe, although they composed 15 percent of the total weight of the fish [7] and firmly packed the body cavity with large eggs. (Random samples of 25 eggs from each measured in a measuring trough had an average diameter of 2.0 millimeters.) The egg size of the Lake Superior fish was about the same as that of 2 pygmy whitefish from the spawning run in Bull Lake, Montana. In the Bull Lake fish the average diameter of 11 residual eggs of a nearly spent female was 2.0 millimeters and the average diameter of the eggs of a nearly ripe fish was 2.1 millimeters. Testes of Lake Superior males were not yet ripe in the October collection (not milky in color, as were those of the spawning Bull Lake fish). The gonads of 2 spent, mature males and 2 females collected January 11 appeared to have recovered fully from spawning. The testes were not milky and were smaller than in fish of the October collections. Some of the 15 residual mature eggs found in the ovaries of one of the females were discolored and disfigured; apparently resorption had begun.

---

[7] The average percentage of the total weight made up by ovaries of 25 mature females collected in Keweenaw Bay on October 15 was also 15.

In comparison with the November or December spawning of pygmy whitefish in Lake Superior, fish caught in Bull Lake (Weisel and Dillon, 1954) were in breeding condition during the December 26–January 12 period. Kendall (1921) found Alaska fish of this species in spawning condition in one collection in August and in another (from a different locality) in November. Pygmy whitefish caught November 17, 1936, in Glacier National Park, Montana, were in breeding condition and obviously represented a spawning aggregation.

The breeding grounds of the pygmy whitefish in Lake Superior are not known. The capture of young fish in relatively shallow water (13–18 fathoms) at Keweenaw Bay, Point Abbaye, and Siskiwit Bay (Stations 9, 13, and 6) together with the tendency of yearling fish to inhabit the shallower waters of Keweenaw Bay offers some evidence that spawning occurs in shallow water. On the other hand, young fish were caught at 16 to 32 fathoms at Laughing Fish Point (Station 16).

At Bull Lake, Montana, pygmy whitefish in breeding condition were caught in shallow water near the mouth of a tributary stream (Weisel and Dillon, 1954), and the spawning fish from Lake McDonald also were presumably taken in shallow water.

FOOD

Stomach contents were examined from 112 pygmy whitefish 2.4 to 5.9 inches long collected May 7, 1953–January 11, 1954, at 5 stations in Lake Superior. Samples used for food studies were taken at random or comprised all individuals caught in a single drag of the trawl. Because contents of individual stomachs were often too small for satisfactory measurement, a single volume determination (by liquid displacement in a sedimentation tube graduated to 0.01 cubic centimeter) was made for the aggregate of each food item from an entire collection.

Crustacea occurred in 95 percent of the stomachs of pygmy whitefish and composed 77 percent of the total food volume (Table 19). Ostracods and amphipods (principally or entirely *Pontoporeia*), were the chief components, comprising 75 percent of the volume. Ostracods were not found in stomachs from two small collections off Laughing Fish Point but were well represented in fish from other localities. Amphipods occurred in 15 to

TABLE 19. — *Percentage frequency of occurrence and (in parentheses) percentage of total volume composed by food items in stomachs of pygmy whitefish in Lake Superior, 1953*

[All collection dates were in 1953, except for that of January 11, 1954. Tr indicates volume less than 0.5 percent. Taxonomic groups in footnotes show principal components of higher groups.]

Item	Keweenaw Bay			Siskiwit Bay	Apostle Islands	Laughing Fish Point		Total
	May 7-11	Aug. 2	Oct. 15	Sept. 7	May 30, July 29	Oct. 21	Jan. 11, 1954	
Total length (inches)	3.5-5.4	3.9-5.4	2.7-5.2	2.4-4.3	3.7-5.9	2.9-4.9	4.4-5.0	2.4-5.9
Number of stomachs	11	7	41	31	15	3	4	112
Crustacea	100 (85)	100 (82)	100 (94)	87 (68)	100 (93)	100 (95)	50 (1)	95 (77)
Cladocera[1]	...	...	[2]15 (tr)	...	...	[3]67 (tr)	...	7 (tr)
Copepoda[4]	91 (9)	...	12 (tr)	29 (5)	20 (tr)	67 (58)	...	26 (2)
Ostracoda	82 (6)	100 (9)	93 (94)	52 (2)	100 (37)	...	...	76 (31)
Mysidacea[5]	18 (2)	...	...	...	13 (tr)	...	...	4 (tr)
Amphipoda[6]	73 (68)	100 (73)	15 (tr)	58 (61)	100 (56)	67 (37)	50 (1)	52 (44)
Hydracarina	...	...	2 (tr)	...	...	...	...	1 (tr)
Insecta	36 (tr)	100 (18)	42 (6)	71 (21)	100 (5)	67 (tr)	50 (1)	62 (9)
Larvae and pupae[7]	36 (tr)	100 (18)	22 (3)	71 (21)	87 (4)	67 (tr)	25 (tr)	52 (8)
Adult[8]	...	29 (tr)	29 (3)	3 (tr)	33 (1)	...	50 (1)	20 (1)
Pelecypoda[9]	...	...	...	42 (11)	53 (2)	33 (5)	...	20 (3)
Fish eggs[10]	46 (15)	...	...	...	...	...	100 (98)	8 (11)

[1] *Daphnia* [2] Ephippia presumed to be of *Daphnia* [3] Both ephippia and adult *Daphnia* [4] *Cyclops, Mesocyclops, Epischura, Senecella, Diaptomus, Limnocalanus* [5] *Mysis* [6] *Pontoporeia* [7] *Cryptochironomus, Prodiamesa* [8] Hymenoptera, Diptera, Hemiptera, Coleoptera [9] *Pisidium conventus* [10] *Coregonus*

100 percent of the stomachs in the different collections and composed from 1 to 73 percent of the total volume. As many as 285 ostracods or 140 amphipods occurred in a single stomach. Copepods were in 26 percent of the stomachs (2 percent of the total volume) but were usually incidental in the diet of fish more than 3.5 inches long. Cladocera (partly in the form of ephippia, presumably of *Daphnia* or closely related forms) and *Mysis* (which was known to be abundant at several of the collection stations) were unimportant items.

Insects were found in 62 percent of the stomachs and made up 9 percent of the food of pygmy whitefish. Larvae and pupae of aquatic forms (principally Chironomidae) occurred in all collections and in 52 percent of the stomachs but composed only 8 percent of the total volume and did not exceed 21 percent of the food volume in any single collection. Adult insects (undoubtedly taken on or near the lake bottom) were present in 20 percent of the stomachs but made up only 1 percent of the volume. Of the other invertebrates found, larval clams (Sphaeriidae) occurred in 20 percent (3 percent of the volume). Only a single Hydracarina was found.

Fish eggs, presumably coregonine, occurred in the collections of May 7–11 (46-percent frequency of occurrence; 15 percent of the volume) and January 11 (in each of 4 stomachs containing food and comprising 98 percent of the total volume). As many as 30 whole eggs and 29 egg shells were in a single stomach in the January 11 collection. Stomach contents of fish on this date were thus markedly different from those of 3 stomachs collected at the same station on October 21, when copepods and amphipods were the principal food. When available, fish eggs are perhaps important in the diet of pygmy whitefish. In support of this conjecture, Kendall (1921) found from 1 to 18 small salmonid eggs in stomachs of 4 of 5 pygmy whitefish collected at Lake Aleknagik, Alaska, August 2, 1912.

Small quantities of finely divided organic detritus were found in 8 of 21 stomachs that were collected in May. (Possibly this material was equivalent to the "indeterminable mush" reported by Kendall [1921] in stomachs of four pygmy whitefish collected in Lake Aleknagik, Alaska, July 20, 1909.) Sand grains—as many as 27 in a single stomach—were present in 10 of the 112 fish examined.

That copepods are extremely important to small fish was shown by stomach analyses of 5 young individuals collected off Point Abbaye (Station 13) on September 10, 1953, and 12 caught in Siskiwit Bay (Station 6) on September 7 (data not shown in Table 19). Their diet was composed almost entirely of copepods (18 to 144 per stomach); in addition, chironomid larvae and pupae contributed a small proportion of the food of the fish from Point Abbaye and a single cladoceran occurred in stomachs of each of 2 of the 12 fish from Siskiwit Bay.

ASSOCIATED SPECIES

Twelve species or groups of species (the latter not specifically identified) were collected with the pygmy whitefish in Lake Superior. Estimates of the "degree of association" have been made in terms of percentage occurrence in trawl hauls that took pygmy whitefish and percentage occurrence at stations (and on the same dates and depths) at which *Coregonus coulteri* was collected (Table 20).

The most common associates of the pygmy whitefish were cottids, which occurred in 87 percent of the hauls and at 88 percent of the stations. The species taken most often was *Cottus cognatus; Myoxocephalus quadri-*

TABLE 20. — *Associates of the pygmy whitefish in Lake Superior*

[The ranking of each species or group of species is expressed in terms of its percentage frequency of occurrence in 99 trawl hauls and at 17 stations where pygmy whitefish were taken]

Species	Percentage frequency of occurrence	
	In individual hauls	At stations
Cottidae (*Cottus cognatus, C. ricei, Myoxocephalus quadricornis*)	87	88
Ninespine stickleback (*Pungitius pungitius*)	81	76
American smelt (*Osmerus mordax*)	63	59
Shallowwater cisco (*Coregonus artedii*)	36	71
Chubs (*Coregonus hoyi, C. reighardi, C. zenithicus,* possibly *C. kiyi*)	36	65
Lake trout (*Salvelinus namaycush*)	57	41
Trout-perch (*Percopsis omiscomaycus*)	34	41
Unidentified coregonines (chubs and /or ciscoes)	34	35
Burbot (*Lota lota*)	18	18
Longnose sucker (*Catostomus catostomus*)	15	12
White sucker (*Catostomus commersoni*)	4	12
Lake whitefish (*Coregonus clupeaformis*)	2	6
Chestnut lamprey (*Ichthyomyzon castaneus*)	1	6
Yellow perch (*Perca flavescens*)	0	6

cornis[8] occurred in numbers only in the deeper waters. The ninespine stickleback was next in importance (81 percent of the hauls; 76 percent of the stations), followed by the smelt, shallowwater cisco (lake herring), and chubs. The latter group was composed of 3 (possibly 4) species. Ciscoes, chubs, and *Coregonus* spp. (unidentified small specimens), when considered as a group, occurred in 84 percent of the hauls and at 88 percent of the stations. Lake trout and trout-perch were other important associates of the pygmy whitefish. Longnose suckers, burbot, lake whitefish, white suckers, chestnut lampreys, and yellow perch were much less common, occurring only in occasional trawl hauls or collection stations. Absent from the list was the round whitefish, closest relative of the pygmy whitefish in Lake Superior (chiefly a resident of shallower waters). With the exception of four young (1.5 to 1.6 inches in total length) caught in the Apostle Island region on July 29, 1953, and a 3.5-inch yearling caught west of Grand Marais, Michigan, on June 14, 1953, *Coregonus cylindraceus* was not taken by trawling in Lake Superior. The Cyprinidae, Percidae, and Centrarchidae, dominant groups of American fishes, are notable for their scarcity or absence in the deep cold waters of Lake Superior where *C. coulteri* lives.

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[8] The fourhorn sculpin, better known to most North American ichthyologists as the deepwater sculpin, *Triglopsis thompsoni* Girard, is chiefly a circumpolar marine fish. In certain large lakes in northern Europe and North America there occur isolated populations that are presumably relicts of independent invasions from the sea near the close of the Pleistocene. This freshwater ecotype contrasts with the saltwater fish in the smaller size, the reduction in number and development of ossified plates on the body, and the weakening or loss of the four rugose ridges or knobs on the top of the head (Berg and Popov, 1932; Berg, 1949). A number of subspecies have been established on variations, mainly in the characters mentioned (Berg and Popov, 1932). Whether or not any of these have a genetic basis is a matter for conjecture. The populations from Lake Onega, Russia, and the Great Lakes are strikingly similar. Until the nature of the variations is more clearly understood we concur with Vladykov (1933) in adopting the binomial designation for all populations of *Myoxocephalus quadricornis* (Linnaeus).

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The Movement and Recovery of Tagged Walleyes in Michigan, 1929-1953

by

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THE MOVEMENT AND RECOVERY OF TAGGED WALLEYES IN MICHIGAN, 1929-1953

By

Paul H. Eschmeyer and Walter R. Crowe

INTRODUCTION

A report of field and laboratory studies on the life history of the walleye, *Stizostedion vitreum vitreum* (Mitchill), was published in 1950 as Bulletin No. 3 of the Institute for Fisheries Research. The present paper is a revision of, and supplement to, the section on migration (pp. 76–90) in the earlier work, with the addition of four years of observations on studies begun prior to 1950, as well as a record of results from the tagging of 1,383 walleyes in six experiments initiated since the publication of the Bulletin. It thus summarizes results of the tagging of 14,137 walleyes in Michigan during the quarter-century, 1929–1953. Since tagging studies begun in 1953 are not included, all experiments have been observed for two or more fishing seasons. In addition to analyses of tag returns, data are presented on the effect of jaw tags on growth and condition.

Walleyes for tagging were collected by trap nets and dip nets, usually during the spawning season. Tags were attached to either the upper or lower jaw, except during the period 1929–1932, when they were placed on the gill cover. In the years 1939–1946, walleyes were tagged on the lower jaw (technique described by Shetter, 1936); in 1947 and 1948, fish were marked on either the upper or lower jaw; and in 1949 and subsequent years, they were marked on the upper jaw, with No. 3 strap tags passing around the maxillary and premaxillary.[1] Rewards were not offered for the return of tags. Walleyes were marked in a number of waters scattered widely throughout the state, although most were tagged in waters of the Muskegon River drainage in the Lower Peninsula and in Lake Gogebic in the Upper Peninsula. The several localities where tagged fish were released are shown in Figure 1.

In order to facilitate analysis of recovery data, tagged walleyes recaptured between the date of marking and December 31 of the same year were considered first-year returns in this report; subsequent recoveries were tabulated by calendar years. Since the spawning season (during which most of the walleyes were tagged) precedes most of the fishing season in Michigan, the omission of about the first four months from the first "year" after tagging had little effect on comparisons of the rate of recapture during the first season with that during later full years. A different procedure was employed in Bulletin No. 3, where most returns were considered with reference to each anniversary date of tagging. A few records were added to those already reported in the Bulletin for the period prior to 1950, since occasional recoveries have been reported by anglers as much as a year after the date of recapture of marked fish.

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[1] In 1947, 435 walleyes marked on the upper jaw with the No. 3 strap tag, 160 marked on the lower jaw with this tag, and 855 tagged on the lower jaw with larger (No. 18) jaw tags, were released in various waters of the Muskegon River drainage. Subsequent returns did not demonstrate a statistically significant difference in the rate of recovery among walleyes marked by these three methods. No. 3 tags are applied more readily on the upper jaw than on the lower jaw of large walleyes, and they are not known to cause serious abrasion of the jaw or loss of condition (see p. 26) which may be associated with the use of the No. 18 tags. The large tags are about twice as long and six times as heavy as the No. 3 strap tags.

The cooperation of many sport and commercial fishermen who reported recoveries of tagged walleyes is acknowledged. Several employees of the Michigan Department of Conservation assisted in the field work of the various tagging experiments. The tagging of 249 walleyes in Crooked Lake during the winter of 1952 was under the direct supervision of R. F. Sharkey. G. P. Cooper and Ralph Hile read the manuscript and offered suggestions. William Cristanelli prepared the illustrations.

Early Tagging Experiments, 1929–1932

During the years 1929–1932, 2,783 walleyes were marked with strap tags attached to the gill covers, and released in five localities Of these, 37 (1.3 percent) were subsequently recovered by anglers (Table 1).

Only one recovery resulted from the tagging of 177 walleyes in Saginaw Bay in 1929; 1 of 14 was recovered in Hamlin Lake in 1930; and none of 53 walleyes tagged in Van Etten Lake in 1931 was caught. Returns were little better (1.4 percent) from 213 walleyes tagged in 1931, and from 2,154 marked in 1932, which were transferred from the Cheboygan River below Cheboygan Dam to the upstream lakes and connecting waters which together comprise the Inland Waterway System (Fig. 3, p. 21). Some of the marked fish moved extensively during the interval between time of tagging and recapture. One walleye released immediately above Cheboygan Dam was recaptured in Crooked Lake (a minimum distance of 32 miles). Two other fish which were transferred to Crooked Lake moved in the opposite (downstream) direction a similar distance, before they were recovered near the dam. Although all four recoveries of tagged walleyes released in Burt Lake were made in that lake, some fish released at other localities in the Inland Waterway had moved to connecting lakes or streams or had passed Cheboygan Dam and returned to Lake Huron before they were recaptured.

Table 1.—Number and Percentage (in parentheses) of Tagged Walleyes Recovered in Michigan, 1929–1932*

Locality of release	Year	Number tagged	Recoveries†
Saginaw Bay, Lake Huron	1929	177	1 (0.6)
Hamlin Lake	1930	14	1 (7.1)
Van Etten Lake	1931	53	0 (0.0)
Inland Waterway	1931	213	3 (1.4)
Inland Waterway	1932	2,154	29 (1.3)
Muskegon River impoundments	1932	172	3 (1.7)
Total	....	2,783	37 (1.3)

*Data compiled by David S. Shetter (unpublished).
†All recoveries were made within 6½ months after tagging.

Three fish were recovered of 172 tagged walleyes transferred in 1932 from the Muskegon River below Newaygo Dam to four upstream impoundments. Of these, two were recaptured in the impoundments in which they had been released (Hardy and Croton); the third was caught after moving downstream past Big Rapids and Rogers dams.

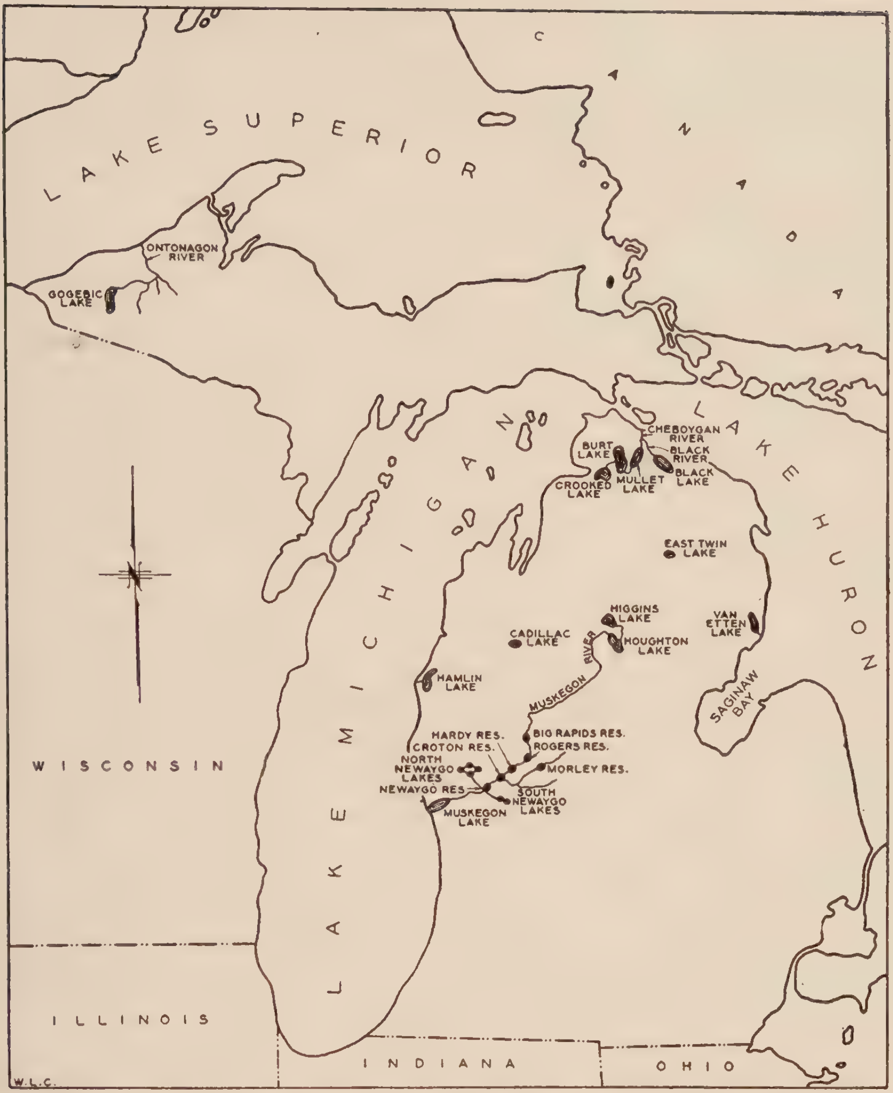
LAKE SUPERIOR
CANADA
ONTONAGON RIVER
GOGEBIC LAKE
LAKE MICHIGAN
LAKE HURON
CHEBOYGAN RIVER
BURT LAKE
BLACK RIVER
BLACK LAKE
CROOKED LAKE
MULLET LAKE
EAST TWIN LAKE
HIGGINS LAKE
HOUGHTON LAKE
VAN ETTEN LAKE
CADILLAC LAKE
MUSKEGON RIVER
HAMLIN LAKE
SAGINAW BAY
HARDY RES.
BIG RAPIDS RES.
CROTON RES.
ROGERS RES.
NORTH NEWAYGO LAKES
MORLEY RES.
NEWAYGO RES.
SOUTH NEWAYGO LAKES
MUSKEGON LAKE
WISCONSIN
ILLINOIS
INDIANA
OHIO
W.L.C.

Figure 1.—Map of Michigan showing localities at which walleyes were tagged (revised from Eschmeyer, 1950).

The early tagging experiments in Michigan demonstrated that walleyes moved considerable distances, and that they were able to pass through or over power dams—two facts corroborated convincingly by later experiments. The failure to obtain more recoveries was undoubtedly due primarily to loss of the opercular tags, soon after application. The longest interval between tagging and recapture was only 6½ months.

TAGGING EXPERIMENTS IN THE MUSKEGON RIVER DRAINAGE

The Muskegon River is a major tributary of southern Lake Michigan (Fig. 1). It originates in Higgins and Houghton lakes and flows in a southwesterly direction for a distance of 227 miles, entering Lake Michigan near Muskegon, by way of Muskegon Lake. Five power dams, ranging in height from 17 to 100 feet and impounding reservoirs ranging in area from 95 acres (Big Rapids Pond) to 3,970 acres (Hardy Pond), are located in the lower 100 miles of the stream.[2]

The earliest walleye tagging experiment conducted in the Muskegon River System (in 1932) is described in the preceding section. Results of more recent studies are summarized in Table 2. In 1939 and 1940, 60 walleyes were tagged in Houghton Lake and 40 were marked in the upper Muskegon River, 1 mile downstream from Houghton Lake (Carbine and Applegate, 1946). During the three years following tagging, 19.0 percent of the fish were recaptured. Recoveries were distributed widely throughout Houghton Lake, and 3 fish were caught approximately 130 miles downstream in the Muskegon River, above and below Big Rapids Dam.

During the period 1947–1952, 4,943 walleyes were tagged in various portions of the Muskegon River drainage. Of these, 832 (16.8 percent) were recovered by the end of 1953 at distances ranging up to 175 miles from the locality of release.

The Newaygo Transfer

The marking of walleyes tagged in the Muskegon River drainage in the years 1947–1952 was part of a research program on the species in the lower reaches of the river and in its impoundments. Each year large numbers of walleyes on their spring spawning migration move up the Muskegon River and congregate (usually in April) below Newaygo Dam, an impassable barrier to upstream movement located 39 miles above the mouth of the river. Each year since 1923 (except 1951), varying numbers of walleyes and smaller numbers of other game fish have been captured with dip nets below the dam and transported to upstream impoundments or to other waters of the drainage, in an operation which has become known as the "Newaygo transfer." In 1928, the Michigan Department of Conservation undertook the supervision of the netting and transfer of the fish. Since that time the numbers of fish conveyed around the barrier have ranged from 469 (1928) to 43,088 (1933) and have averaged 8,683 per year.[3]

The Newaygo transfer has been a source of controversy almost since the year of its inception and was the subject of litigation as recently as 1952. Many persons and organizations interested in the walleye fishery in the impoundments favor the annual transfer, whereas many interested primarily in the fishery in the lower Muskegon River or Muskegon Lake strongly oppose its continuation. With the objective of obtaining facts with a bearing

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[2] The dams, their heights, and the areas of the reservoirs are as follows (data by Consumers Power Company): Newaygo—18 feet, 130 acres; Croton—40 feet, 1,380 acres; Hardy—100 feet, 3,970 acres; Rogers—39 feet, 608 acres; Big Rapids—17 feet, 95 acres.

[3] The years of the Newaygo transfer and the number of walleyes transferred are as follows:

1928—469
1929—3,680
1930—8,327
1931—1,547
1932—3,151
1933—43,088
1934—24,284
1935—24,241
1936—6,676
1937—6,931
1938—7,020
1939—6,345
1940—2,641
1941—12,460
1942—12,469
1943—13,186
1944—3,318
1945—789
1946—4,380
1947—5,537
1948—4,743
1949—1,483
1950—2,654
1951—0
1952—10,000
1953—7,661

Table 2—Number and Percentage (in parentheses) of Tagged Walleyes Recovered by Fishermen in the Muskegon River Drainage, 1939-1953

Locality of release	Date tagged		Number tagged	Year after tagging†							Total
	Month*	Year		1	2	3	4	5	6	7	
Houghton Lake‡	4, 5, 6, 7	1939	21	1 (4.8)	. . .	2 (9.5)	. . .	. . .	. . .	. . .	3 (14.3)
	3, 4, 5, 6, 7	1940	39	4 (10.3)	3 (7.7)	. . .	. . .	. . .	. . .	. . .	7 (17.9)
Upper Muskegon River‡	4, 5, 6, 7	1939	16	1 (6.3)	3 (18.7)	1 (6.3)	. . .	. . .	. . .	. . .	5 (31.3)
	3, 4, 5, 6, 7	1940	24	. . .	3 (12.5)	1 (4.2)	. . .	. . .	. . .	. . .	4 (16.7)
Muskegon River Impoundments§	4	1947–1950	3,371	563 (16.7)	39 (1.2)	11 (0.3)	1 (0.0)#	3 (0.1)	. . .	. . .	617 (18.3)
Hardy Pond	5, 6, 7, 8, 9	1948	296	7 (2.4)	13 (4.4)	6 (2.0)	5 (1.7)	2 (0.7)	. . .	– – –	33 (11.1)
	8	1952	99	3 (3.0)	4 (4.0)	– – –	– – –	– – –	– – –	– – –	7 (7.1)
Newaygo Pond	7	1948	6	1 (16.7)	1 (16.7)	. . .	. . .	. . .	. . .	– – –	2 (33.3)
Lower Muskegon River	4	1948	292	32 (11.0)	13 (4.5)	1 (0.3)	1 (0.3)	1 (0.3)	2 (0.7)	– – –	50 (17.1)
	4	1950	473	11 (2.3)	21 (4.4)	6 (1.3)	8 (1.7)	– – –	– – –	– – –	46 (9.7)
Muskegon Lake	3	1948	23	5 (21.7)	. . .	. . .	. . .	. . .	. . .	– – –	5 (21.7)
	4	1952	8	. . .	. . .	– – –	– – –	– – –	– – –	– – –	0 (0.0)
North Newaygo Lakes	4	1947	200	42 (21.0)	8 (4.0)	4 (2.0)	. . .	1 (0.5)	. . .	. . .	55 (27.5)
South Newaygo Lakes	4	1947	175	9 (5.1)	3 (1.7)	1 (0.6)	1 (0.6)	1 (0.6)	. . .	1 (0.6)	16 (9.1)
Total	. . .	. . .	5,043	679 (13.5)	111 (2.2)	33 (0.7)	16 (0.3)	8 (0.2)	2 (0.0)#	1 (0.0)#	850 (16.9)

*Months are numbered consecutively from March (3) to September (9).

†First year extends from the date of tagging through December 31 of the same year; subsequent intervals refer to later calendar years. In the body of the table, "..." indicate no recoveries during year, "– – –" indicate that recoveries could not have been expected because the experiment was not in progress.

‡From Carbine and Applegate, 1946.

§For detailed records, see Table 3.

#Less than 0.05 percent.

on this problem, 3,371 walleyes were jaw-tagged before transfer to the various impoundments in 1947, 1948, and 1950. The results of these experiments are summarized in Tables 3 and 4.

Rate of Recovery of Tagged Walleyes Transferred to Upstream Impoundments

The number and percentage of recoveries of marked walleyes by sport fishermen and commercial operators (the latter only in Lake Michigan) are given in Table 3. Of 1,375 walleyes tagged in 1947, 209 (15.2 percent) were recovered during the first year after tagging, 20 (1.5 percent) during the second year, eight (0.6 percent) in the third year, and three (0.2 percent) in the fifth year (1951). No recoveries were reported in 1950, 1952, or 1953. Recoveries for the seven years following tagging equaled 240 (17.5 percent).

A total of 258 (17.5 percent) of 1,475 walleyes distributed among the impoundments in 1948 were recovered during that year; 16 (1.1 percent) were caught during the following year; one fish was recovered in 1950; and one in 1951 (none in 1952 or 1953). The returns for the six-year period following tagging totaled 276 (18.7 percent).

The release of 521 tagged walleyes in upstream impoundments in 1950 resulted in the recapture of 96 (18.4 percent) during that year, three in 1951, and two in 1952 (none in 1953). Returns for the four-year period numbered 101 (19.4 percent).

Hardy Pond, the largest and deepest of the reservoirs, consistently provided the highest rate of return from the three groups of fish tagged. The average recovery percentage was 27.0 and the range was narrow—26.3 (1950) to 28.0 (1947). The value of 28.0 is the highest rate of return recorded to date for walleyes tagged in Michigan waters.[4] The percentage was undoubtedly influenced by the unusual success of a single fisherman, who caught 57 tagged walleyes which had been released in Hardy Pond during the three years.

The mean rate of recapture for walleyes transferred to Big Rapids Pond was 19.4 percent (range, 17.0 in 1948 to 20.8 in 1947). The recovery rate fluctuated widely in Croton Pond, from 13.9 percent for fish tagged in 1950 to 22.7 percent for fish marked in 1948 (average for the three years of tagging, 18.3 percent). Returns from fish released in Rogers Pond averaged 15.3 percent for the three years (range, 12.2–20.0) and recoveries from marked fish released in Newaygo Pond were poorest of the group (average, 13.0 percent; range, 7.0–18.0).

One lot of 100 tagged walleyes released in 1948 in Morley Pond, a small impoundment on the east branch of the Muskegon River, resulted in the recovery of 14 fish (14.0 percent).

The pattern of recovery exhibited in the tagging experiments in 1947, 1948, and 1950 (after seven, six, and four years of observation) indicate that few additional recaptures can be expected. The average percentage of recovery to date, for the three years of tagging, for all impoundments combined, is 18.5 percent; returns from each year's tagging are within the narrow range of 17.5 (1947) to 19.4 (1950) percent. A total of 617 (18.3 percent) of the 3,371 fish tagged were recaptured. These rates of return are high in comparison with recoveries of walleyes in other Michigan waters and have been exceeded in only one experiment in which more than 100 fish were tagged.[5]

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[4] An exception is shown in Table 2, for native fish released in Newaygo Pond in 1948; but there only six fish were tagged.

[5] The release of 200 marked walleyes in the north Newaygo lakes in 1947 resulted in a recapture rate of 27.5 percent (see p. 18).

TABLE 3—NUMBER AND PERCENTAGE (IN PARENTHESES) OF TAGGED WALLEYES RECOVERED BY FISHERMEN IN MUSKEGON RIVER IMPOUNDMENTS, 1947–1953*

Impoundment of release	Number tagged	Year after tagging†					Total
		1	2	3	4	5	
Tagged in 1947							
Big Rapids...	24	5 (20.8)	...	...	...	...	5 (20.8)
Rogers.......	500	59 (11.8)	2 (0.4)	...	...	...	61 (12.2)
Hardy.......	200	53 (26.5)	3 (1.5)	...	...	...	56 (28.0)
Croton.......	501	76 (15.2)	10 (2.0)	4 (0.8)	...	1 (0.2)	91 (18.2)
Newaygo.....	150	16 (10.7)	5 (3.3)	4 (2.7)	...	2 (1.3)	27 (18.0)
Total......	1,375	209 (15.2)	20 (1.5)	8 (0.6)	...	3 (0.2)	240 (17.5)
Tagged in 1948							
Big Rapids...	200	33 (16.5)	1 (0.5)	...	...	...	34 (17.0)
Rogers.......	275	37 (13.5)	1 (0.4)	...	...	...	38 (13.8)
Hardy.......	300	75 (25.0)	5 (1.7)	...	...	...	80 (26.7)
Croton.......	300	68 (22.7)	...	...	...	...	68 (22.7)
Newaygo.....	300	32 (10.7)	8 (2.7)	1 (0.3)	1 (0.3)	...	42 (14.0)
Morley.......	100	13 (13.0)	1 (1.0)	...	...	...	14 (14.0)
Total......	1,475	258 (17.5)	16 (1.1)	1 (0.1)	1 (0.1)	...	276 (18.7)
Tagged in 1950							
Big Rapids...	132	27 (20.5)	...	...	...	---	27 (20.5)
Rogers.......	50	10 (20.0)	...	...	...	---	10 (20.0)
Hardy.......	167	42 (25.1)	2 (1.2)	...	...	---	44 (26.3)
Croton.......	115	16 (13.9)	...	...	...	---	16 (13.9)
Newaygo.....	57	1 (1.8)	1 (1.8)	2 (3.5)	...	---	4 (7.0)
Total......	521	96 (18.4)	3 (0.6)	2 (0.4)	...	---	101 (19.4)
Grand total.	3,371	563 (16.7)	39 (1.2)	11 (0.3)	1 (0.0)‡	3 (0.1)	617 (18.3)

*This table includes recoveries by sport and commercial fishing, but excludes 25 recoveries (23 in dip nets, one in a seine, and one in a gill net) which are included in Table 4, p. 13. No recaptures were reported during the sixth year after tagging. In the body of the table, ". . ." indicate no recoveries during year, "– – –" indicate that recoveries could not have been expected because the experiment was not in progress.

†First year extends from date of tagging to December 31 of that year; subsequent intervals refer to later calendar years.

‡Less than 0.05 percent.

The average recovery rate from the three lots of tagged fish transferred to the impoundments is more than double the total return to date (8.6 percent) from 6,311 jaw-tagged walleyes in Michigan waters outside the Muskegon River drainage.

Rate of Recovery of Tagged Walleyes in the Muskegon River Below Newaygo Dam

A total of 292 walleyes were tagged and released in the Muskegon River below Newaygo Dam during the 1948 spawning season and 473 were released there in 1950. Of the walleyes released below the dam in 1948, 32 (11.0 percent) were recovered during the first fishing season (Table 2), 13 (4.5 percent) in 1949, one each in 1950, 1951, and 1952, and two in 1953, or a total recovery of 50 (17.1 percent). The walleyes tagged below Newaygo Dam in 1950 yielded a return of 11 (2.3 percent) during the first year after tagging, 21 (4.4 percent) during the second, six (1.3 percent) during the third, and eight

(1.7 percent) during the fourth year after release. Of the 96 recoveries to date from the two lots of fish, 42 were caught in the section of river between Newaygo Dam and Muskegon Lake, and 16 were caught in Muskegon Lake. The remaining 38 returned to Lake Michigan before recapture by anglers (17) or by commercial fishermen (21).

Although a few additional recoveries may be expected, particularly from the fish tagged in 1950,[6] it is doubtful whether the percentage of recovery by fishermen (12.5 percent, 1948 and 1950 data combined) will equal that obtained from tagged walleyes transferred to the upstream impoundments during these same years (18.9 percent). However, the 17.1 percent return from walleyes released below Newaygo Dam in 1948, taken alone, compares well with the rate of recovery in the impoundments.

Tagged walleyes released in the river below Newaygo Dam contributed to the fishery over a longer period of years than did fish transferred to the impoundments. Among tagged fish transferred to the reservoirs, 91 percent of the recoveries made to date were during the first year after tagging; in the lower river this percentage was only 45. Nearly 20 percent of the recoveries in the lower river were during the third or later fishing season following release.

In addition to the walleyes tagged in the Muskegon River below Newaygo Dam, 23 were marked in Muskegon Lake in 1948 and eight were tagged there in 1952. Of these, five have been recovered (Table 2).

Movement of Tagged Walleyes

Walleyes transferred to upstream waters from the Muskegon River below Newaygo Dam showed a marked proclivity to move downstream past the power dams toward their original habitat (Table 4). Fish negotiated each of the five structures in numbers, and the combined data for 1947, 1948, and 1950 tagging show that fewer tagged fish released in three impoundments (Big Rapids, Rogers, and Newaygo) were caught within these reservoirs than were recaptured in downstream waters.

No fish transferred to Big Rapids Pond (the impoundment farthest upstream) during the three years of tagging was recovered in this reservoir. All had moved downstream past the dam; 71.2 percent were caught in Rogers Pond (the next downstream), 21.2 percent in Hardy, 3.0 percent in Croton, and three fish released in Big Rapids Pond in 1950 were reported caught later that year in Muskegon Lake, after moving downstream more than 90 miles and passing each of the five dams.

A total of 31 (28.4 percent) of 109 recoveries of fish released in Rogers Pond were caught in this impoundment; 66.1 percent had moved to Hardy; and 5.5 percent to Croton. The percentage of the total recoveries made within Rogers Pond varied from 9.8 percent of the fish stocked in 1947 to 47.4 percent of the 1948 planting and 70.0 percent of the fish released there in 1950. No fish transferred to this reservoir has been recovered downstream from Croton Dam.

More than 90 percent of the 181 recoveries of tagged walleyes released in Hardy Pond have been made in this impoundment; among the three groups stocked this proportion has varied within the narrow limits of 85.7 and 93.8 percent. Thirteen (7.2 percent) of the recoveries were in Croton Pond and five (2.8 percent) were in waters downstream from Newaygo Dam.

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[6] Fishermen had recovered four fish of this lot by November 1, 1954, after the preparation of this manuscript.

TABLE 4—NUMBERS AND PERCENTAGES (IN PARENTHESES) OF TAGGED WALLEYES RECOVERED AT VARIOUS LOCALITIES AFTER TRANSFER FROM THE MUSKEGON RIVER BELOW NEWAYGO DAM TO FIVE UPSTREAM IMPOUNDMENTS, 1947–1953

Impoundment of release	Year	Number tagged	Number of recoveries	Locality of recovery*					
				Big Rapids	Rogers	Hardy	Croton	Newaygo	Downstream from Newaygo Dam†
Big Rapids...	1947	24	5	. . .	. . .	4 (80.0)	1 (20.0)	. . .	. . .
	1948	200	34	. . .	24 (70.6)	10 (29.4)	. . .	. . .	. . .
	1950	132	27	. . .	23 (85.2)	. . .	1 (3.7)	. . .	3 (11.1)
	Total	356	66	. . .	47 (71.2)	14 (21.2)	2 (3.0)	. . .	3 (4.6)
Rogers......	1947	500	61	– – –	6 (9.8)	50 (82.0)	5 (8.2)	. . .	. . .
	1948	275	38	– – –	18 (47.4)	19 (50.0)	1 (2.6)	. . .	. . .
	1950	50	10	– – –	7 (70.0)	3 (30.0)	. . .	. . .	. . .
	Total	825	109	– – –	31 (28.4)	72 (66.1)	6 (5.5)	. . .	. . .
Hardy.......	1947	200	56	– – –	– – –	48 (85.7)	6 (10.7)	. . .	2 (3.6)
	1948	300	80	– – –	– – –	75 (93.8)	5 (6.2)	. . .	. . .
	1950	167	45	– – –	– – –	40 (88.9)	2 (4.4)	. . .	3 (6.7)
	Total	667	181	– – –	– – –	163 (90.1)	13 (7.2)	. . .	5 (2.8)
Croton......	1947	501	101	– – –	– – –	– – –	67 (66.3)	3 (3.0)	31 (30.7)
	1948	300	68	– – –	– – –	– – –	66 (97.1)	2 (2.9)	. . .
	1950	115	18	– – –	– – –	– – –	15 (83.3)	. . .	3 (16.7)
	Total	916	187	– – –	– – –	– – –	148 (79.1)	5 (2.7)	34 (18.2)
Newaygo....	1947	150	30	– – –	– – –	– – –	– – –	6 (20.0)	24 (80.0)
	1948	300	49	– – –	– – –	– – –	– – –	8 (16.3)	41 (83.7)
	1950	57	6	– – –	– – –	– – –	– – –	. . .	6 (100.0)
	Total	507	85	– – –	– – –	– – –	– – –	14 (16.5)	71 (83.5)

Total number of walleyes recovered after passing barriers, 1947–1953‡..66 97 29 47 113

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*This table includes 25 recoveries (23 in dip nets, 1 in a seine, and 1 in a gill net) which are not included in Tables 2 and 3. In the body of the table, ". . ." indicate no recoveries, "– – –" indicate that recoveries could not have been expected because the reservoir is situated upstream from the locality of release.

†Downstream waters include the Muskegon River below Newaygo Dam, Muskegon Lake, or Lake Michigan.

‡The line dividing the columns represents the dam between adjacent impoundments.

A total of 79.1 percent of the recoveries of walleyes stocked in Croton Pond were recovered in this impoundment; 2.7 percent were recaptured in Newaygo Pond; and 18.2 percent had negotiated both Croton and Newaygo dams before recapture. Results varied among the three lots of tagged fish. More than one-third of the fish recovered from the 1947 release were caught in downstream waters, whereas this barrier was passed by only two of 68 fish which were recovered after the 1948 tagging.

Only 16.5 percent of 85 recoveries of walleyes released in Newaygo Pond were made in this water; the remainder had moved downstream past the dam.

The following percentages of walleyes transferred to upstream reservoirs from the Muskegon River below Newaygo Dam had returned to their original habitat by the time of their recapture: Big Rapids Pond—4.6 percent (none in 1947 or 1948); Rogers Pond—none; Hardy Pond—2.8 percent (none in 1948); Croton Pond—18.2 percent (none in 1948); and Newaygo—83.5 percent. Of 3,271 walleyes transferred to the five impoundments, 628 have been recovered to date by angling and dip netting; 113, or 18 percent had returned to points below the farthest downstream barrier and regained unhindered access to Lake Michigan.

The degree of difficulty of passing power dams in the Muskegon River appears to vary widely, presumably as a result of differences in height and construction. The variation in the percentages of recoveries made at downstream localities may be related also to differences in the suitability of each of the reservoirs for walleyes, and differences in the fishing pressure on each. Table 4 provides the data for rating the five dams with respect to loss of transferred fish. It is based on the total known instances of fish passing each structure, and the percentage of marked fish stocked in each pond which had escaped from it before recovery. On this basis, Big Rapids Dam was passed most readily (66 passages and a 100 percent loss of fish to downstream waters before recapture). Newaygo Dam was next (113 passages and an 83.5 percent loss of fish), followed by Rogers (97 passages and a 71.6 percent loss), Croton (47 passages and a loss of 20.9 percent), and Hardy (29 passages and a 10.0 percent loss).

Many fish had passed two or more dams before they were recaptured (Table 4). As noted above, three fish released in Big Rapids Pond passed all five of the dams before recapture. Seven tagged walleyes passed three dams (two negotiated Big Rapids, Rogers, and Hardy, and five passed Hardy, Croton, and Newaygo). Fourteen tagged walleyes passed both Big Rapids and Rogers dams before recapture; six passed Rogers and Hardy; and 34 negotiated Croton and Newaygo. Two fish (data not included in Table 4) moved from Morley Pond to the next downstream impoundment, Croton Pond.

That the movement of fish downstream through the dams may have been accompanied by some mortality is suggested by Table 3, which shows not only that the percentage of recovery during years after the year of tagging was small, but that there was a tendency for this percentage to vary inversely with the distance of the impoundment from Lake Michigan. In view of the inclination for transferred walleyes to pass downstream through the dams, one may suspect (as suggested by Eschmeyer, 1950) that the hazards to survival multiply with the number of dams which must be passed to reach the original habitat. The fish which were able to move out of the impounded section of the stream provided 65 percent of the returns during the years following that of tagging; few walleyes survived in the impoundments to provide fishing during years subsequent to that of release. To date, 528 of 617 recoveries (85.6 percent) by anglers of walleyes which have been transferred to the reservoirs have been made within the impounded section of the river. However, only 19 (3.6 percent) of these recaptures have been in the impounded waters during the year following that of tagging (Table 5), and no fish has been recovered in any water upstream from the lowest barrier more than 15 months after the date of transfer. In contrast, 35 recoveries have been made after the year of tagging in downstream waters (20 during the second year, 11 during the third, one during the fourth, and three during the fifth year after marking).

Table 5.—Localities of Recovery, During the Second Year After Marking, of Tagged Walleyes Transferred to Upstream Impoundments From the Muskegon River Below Newaygo Dam (data for 1947, 1948 and 1950 combined)*

Impoundment of release	Number tagged	Locality of recovery					
		Big Rapids	Rogers	Hardy	Croton	Newaygo	Down-stream waters
Big Rapids....	356	...	...	1	...	...	...
Rogers........	825	...	1	2	...	...	...
Hardy........	667	...	...	10	...	...	...
Croton........	916	...	...	...	2	1	7
Newaygo......	507	...	...	...	...	1	13
Morley........	100	...	...	...	1	...	...
Total.....	3,371	...	1	13	3	2	20

*Data of this table are included in Tables 3 and 4.

That passage through a dam may be hazardous was demonstrated experimentally on August 27, 1952, when six tagged walleyes were passed through a turbine at Croton Dam. One which was recovered dead below the dam a short time later had suffered extensive internal injuries. Prevóst, Legendre, and Lespérance (1944) also noted that some walleyes were killed in passing through a 125-foot power dam in Quebec. Of 46 walleyes (average weight, 3 pounds) marked with cork floats and passed through the turbines, 25 were recaptured below the dam in good condition, eight were injured or killed, and 13 were not recovered.

The localities of recovery of all tagged walleyes transferred to the impoundments or released in the Muskegon River or Muskegon Lake in 1947, 1948, 1950, and 1952 are summarized in Figure 2. Results for the four years of tagging are combined, and recoveries made by dip nets in the Muskegon River below Newaygo Dam are included. The movements of tagged walleyes within the impounded section of the river have already been described (see Table 4).

The tagged walleyes recovered in the section of stream between Newaygo Dam and Muskegon Lake had been released at the following points: Below Newaygo Dam—65 (23 of these in dip nets); in Newaygo Pond—33 (12 in dip nets); in Croton Pond—16 (10 in dip nets); and in Hardy Pond—three (1 in a dip net). Recovered in Muskegon Lake were three fish from Big Rapids Pond, one from Hardy, four from Croton, eight from Newaygo, 16 from below Newaygo Dam, and one from Muskegon Lake. The following tagged walleyes had returned to various portions of Lake Michigan: one from Hardy Pond; 14 from Croton; 30 from Newaygo; 38 from below Newaygo Dam; and four from Muskegon Lake.

The walleyes which moved to Lake Michigan scattered widely along the east shore of the lake; recoveries were made as far south as Porter Beach, Indiana, and as far north as Good Harbor Bay, points which are approximately 250 miles apart.

Nearly all of the tagged walleyes recovered in Lake Michigan (Fig. 2) had moved considerable distances between the dates of release and recovery. The 42 fish caught near the mouth of the Muskegon River had traveled an average of 44 miles (range, 5–60). For other localities south of Muskegon the numbers of fish and distances traveled were: eight near the mouth of the Grand River, 54 miles (range, 50–63); 12 near the mouth of the Kalamazoo River, 86 miles (range, 76–93); five near St. Joseph, Michigan, 123 miles (range, 115–133); three off Bridgman, Michigan, all 137 miles; and two near Porter Beach, Indiana, 114 and 163 miles.

Corresponding data for tagged walleyes which moved north from Muskegon in Lake Michigan are: six at the mouth or immediately north of the White River, 55 miles (range, 47–63); two near Pentwater, Michigan, both 80 miles; three at the mouth of the Pere Marquette River, 87 miles (range, 82–90); two off the Manistee River, 117 and 133 miles; one in Betsie Bay, 140 miles; and one in Good Harbor Bay, 175 miles. The last fish had moved the farthest of any recaptured to date in Michigan. Fourteen walleyes had moved more than 100 miles between the time of release and recapture.

Observations in waters outside Michigan have also shown the walleye to be a far-ranging species. Doan (1942) reported the recovery of a walleye that had moved 200 miles in Lake Erie; Eddy and Surber (1947) stated that tagged walleyes were caught in Minnesota within a few months after release, at distances of 70 to 100 miles from the place of tagging; and Kingsbury (1948) reported that a female walleye tagged in Lake Champlain, New York, was caught 100 miles distant after an interval of 30 days. Of 505 tagged walleyes recaptured within about seven months after transfer from northern Lake Champlain to Chambly Reservoir, in the Richelieu River, Quebec, 20 had traveled distances of 100 to 175 miles (Desrochers, 1953).

Rate of Recovery and Movement of Walleyes Native to the Muskegon River Impoundments

That some walleyes native to the impoundments move downstream through the Muskegon River power dams was inferred by Eschmeyer (1950) on the basis of the occurrence of unusual numbers of small walleyes in Hardy Pond (although growth rate was not stunted), the scarcity of large native fish (particularly sexually mature females), and the observed propensity of transferred fish to move downstream. In 1948, 296 native walleyes averaging 12.8 inches in length were marked in Hardy Pond and 99 (average length, 13.3 inches) were tagged in 1952. Of 33 recoveries from the fish tagged in 1948, 27 were from Hardy Pond (seven in 1948, 13 in 1949, four in 1950, two in 1951, and one in 1952); three fish were recovered in Croton Pond (two in 1950; one in 1952), and three were recovered in 1951 in waters downstream from Newaygo Dam (one at a point seven miles below the dam, and two near the mouth of the Muskegon River). Of seven fish recovered from the 1952 tagging, two were caught in 1952 and three in 1953 in Hardy Pond; one was

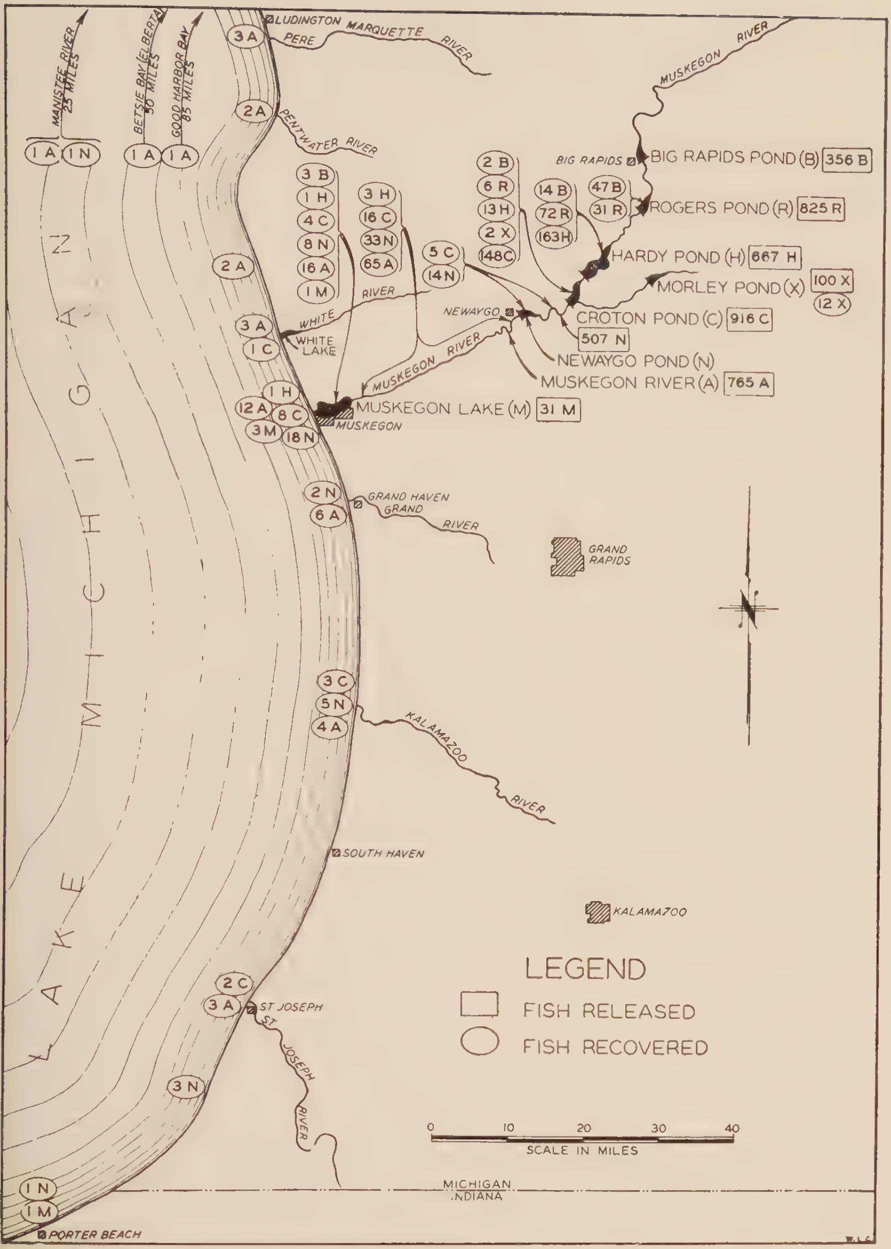
LUDINGTON
PERE MARQUETTE RIVER
MUSKEGON RIVER
MANISTEE RIVER 25 MILES
BETSIE BAY (ELBERTA) 50 MILES
GOOD HARBOR BAY 85 MILES
1 A
1 N
1 A
1 A
3 A
2 A
PENTWATER RIVER
BIG RAPIDS
BIG RAPIDS POND (B) 356 B
2 B
6 R
13 H
2 X
148 C
14 B
72 R
163 H
47 B
31 R
ROGERS POND (R) 825 R
HARDY POND (H) 667 H
MORLEY POND (X) 100 X
12 X
3 B
1 H
4 C
8 N
16 A
1 M
3 H
16 C
33 N
65 A
5 C
14 N
2 A
WHITE RIVER
3 A
1 C
WHITE LAKE
NEWAYGO
CROTON POND (C) 916 C
507 N
NEWAYGO POND (N)
MUSKEGON RIVER (A) 765 A
MUSKEGON RIVER
1 H
12 A
8 C
3 M
18 N
MUSKEGON LAKE (M) 31 M
MUSKEGON
LAKE MICHIGAN
2 N
6 A
GRAND HAVEN
GRAND RIVER
GRAND RAPIDS
N
3 C
5 N
4 A
KALAMAZOO RIVER
SOUTH HAVEN
KALAMAZOO
LEGEND
FISH RELEASED
FISH RECOVERED
2 C
3 A
ST JOSEPH
ST JOSEPH RIVER
3 N
0
10
20
30
40
SCALE IN MILES
MICHIGAN
INDIANA
1 N
1 M
PORTER BEACH
W.L.C.

Figure 2. -Localities of release and of recovery of tagged walleyes released in the Muskegon River and Muskegon Lake. Places of release are designated as follows: B -Big Rapids Pond; R -Rogers Pond; H—Hardy Pond; C—Croton Pond; X—Morley Pond; N—Newaygo Pond; A—Muskegon River below Newaygo Dam; and M—Muskegon Lake (revised from Eschmeyer, 1950).

found dead by a fisherman in Croton Pond, 10 days after tagging; and one was recovered in Croton Pond in 1953.[7]

The pattern and rate of recovery for native walleyes in Hardy Pond were similar to those for native walleyes in Michigan waters outside the Muskegon River drainage, but were markedly different from those of fish transferred to Hardy Pond from the Muskegon River below Newaygo Dam. Total recoveries were much higher for transferred fish (27.0 percent as an average for three years of tagging—see Table 3) than for native fish (10.1 percent for two years of tagging; however, a few additional recoveries may be expected). The proportion of total recoveries made during the first year after tagging was much higher among transferred fish (94.4 percent, 1947, 1948, and 1950 data combined) than native fish (21.2 percent for fish released in 1948, in an experiment which may be considered nearly terminated, since no recoveries were made in 1953).[8] Some native walleyes remained in this reservoir as long as five years (after tagging in 1948) before being recaptured there, whereas no transferred fish have been recovered in the impoundment more than 15 months after tagging. A larger proportion of the recoveries of tagged native fish (20.0 percent, 1948 and 1950 data combined) than of transferred fish (9.4 percent, 1947, 1948, and 1950 data combined) was made in waters downstream from Hardy Pond.

In addition to native walleyes tagged in Hardy Pond, six native walleyes of illegal size were marked in Newaygo Pond in 1948. Of this group, one was retaken during that year in the reservoir and one was recovered in 1949 in the river below Newaygo Dam.

Rate of Recovery and Movement of Tagged Walleyes in the Newaygo Lakes

During the 1947 Newaygo transfer, 200 tagged walleyes were released in the north Newaygo lakes and 175 were transferred to the south Newaygo lakes. To date, seven years after release, 55 (27.5 percent) of the fish transferred to the north Newaygo lakes have been recovered. The tagged fish moved freely among the four relatively deep, clear lakes which comprise this chain, but only one returned to the Muskegon River. In the shallow, weedy south Newaygo lakes returns were fewer (9.1 percent to date); one fish regained access to the river. Returns from fish stocked in the north Newaygo lakes were distributed over five fishing seasons (no recoveries during the fourth year), and returns from fish released in the south Newaygo lakes extended over a period of seven seasons (no recoveries during the sixth year).

Tagging Experiments in the Inland Waterway

The low rate of return from 2,367 walleyes that were tagged on the gill covers before transfer from the Cheboygan River below Cheboygan Dam to the lakes and connecting streams of the Inland Waterway was discussed in an earlier section (p. 6). Results were more satisfactory when 568 jaw-tagged walleyes were released in these waters in 1912 in a repetition of the earlier experiment. Recoveries from that transfer total 61 (11.3 percent)

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[7] Records of recoveries from 251 walleyes, mostly of small size, tagged by a fisherman who caught them on live bait in Hardy Pond in 1949 are not included in the data of Table 2, or elsewhere in this report. Probably high mortality (about 50 percent of the fish were reported released with hooks in their throat or stomach) and inexperienced tagging technique combined to limit the recoveries during the five years after tagging to only two fish. One of these was caught in Hardy Pond in 1949 and the other in Muskegon Lake in 1950.

[8] These percentages are 96.1 and 48.5, respectively, when recoveries of both transferred and native fish are considered in relation to the anniversary date of tagging, rather than by calendar year. This procedure gives a better comparison since some of the native fish were marked as late in the year as September, after much of the fishing season was past.

TABLE 6—NUMBER AND PERCENTAGE (IN PARENTHESES) OF TAGGED WALLEYES RECOVERED BY FISHERMEN IN THE INLAND WATERWAY, MICHIGAN, 1942–1953

Locality of release	Date tagged		Number tagged	Year after tagging†										Total
	Month*	Year		1	2	3	4	5	6	7	8	9	10	
Tagged in 1942														
Cheboygan River....	3, 4	1942	154	3 (1.9)	1 (0.6)	1 (0.6)	. . .	. . .	. . .	. . .	1 (0.6)	. . .	. . .	6 (3.9)
Black Lake.	4	1942	136	5 (3.7)	3 (2.2)	5 (3.7)	1 (0.7)	3 (2.2)	1 (0.7)	1 (0.7)	. . .	. . .	1 (0.7)	20 (14.7)
Mullett Lake	4	1942	87	1 (1.1)	1 (1.1)	3 (3.4)	2 (2.3)	1 (1.1)	. . .	. . .	. . .	. . .	. . .	8 (9.2)
Burt Lake..	4	1942	82	5 (6.1)	2 (2.4)	4 (4.9)	. . .	. . .	. . .	. . .	. . .	. . .	. . .	11 (13.4)
Crooked Lake.....	3	1942	109	7 (6.4)	1 (0.9)	2 (1.8)	2 (1.8)	1 (0.9)	2 (1.8)	. . .	1 (0.9)	1 (0.9)	1 (0.9)	18 (16.5)
Total....	. . .	. . .	568‡	21 (3.7)	8 (1.4)	15 (2.6)	5 (0.9)	5 (0.9)	3 (0.5)	1 (0.2)	2 (0.4)	1 (0.2)	2 (0.4)	64§(11.3)
Tagged in 1948 & 1952														
Burt Lake..	1	1948	300	20 (6.7)	22 (7.3)	4 (1.3)	3 (1.0)	1 (0.3)	. . .	– – –	– – –	– – –	– – –	50 (16.7)
Crooked Lake.....	1, 2, 3, 4	1952	249	28(11.2)	18 (7.2)	– – –	– – –	– – –	– – –	– – –	– – –	– – –	– – –	46 (18.5)
Black River.	5	1952	33	3 (9.1)	4(12.1)	– – –	– – –	– – –	– – –	– – –	– – –	– – –	– – –	7 (21.2)
Total....	. . .	. . .	582	51 (8.8)	44 (7.6)	4 (0.7)	3 (0.5)	1 (0.2)	. . .	– – –	– – –	– – –	– – –	103 (17.7)
Grand total.....	. . .	. . .	1,150	72 (6.3)	52 (4.5)	19 (1.7)	8 (0.7)	6 (0.5)	3 (0.3)	1 (0.1)	2 (0.2)	1 (0.1)	2 (0.2)	167 (14.5)

*Months are numbered consecutively from January (1) to May (5).

†First year extends from date of tagging to December 31 of that year; subsequent intervals refer to later calendar years. In the body of the table ". . ." indicate no recoveries during year, "– – –" indicate that recoveries could not have been expected because the experiment was not in progress.

‡All walleyes tagged in 1942 were transferred from the Cheboygan River, below Cheboygan Dam.

§Includes one recovery during fourth year after tagging, on which data are incomplete.

to date. The number and percentage of recoveries from this experiment, together with those from three more recent tagging studies in the Inland Waterway are shown in Table 6.

Among tagged fish transferred to the Inland Waterway in 1942, returns were lowest (3.9 percent) from 154 walleyes stocked in the Cheboygan River above the dam, and highest (16.5 percent) from 109 fish released in Crooked Lake. Eight returns (9.2 percent) were reported from 87 fish stocked in Mullett Lake, 11 (13.4 percent) from 82 released in Burt Lake and 20 (14.7 percent) from 136 walleyes transferred to Black Lake.

The rate and pattern of recovery of transferred fish in the Inland Waterway was markedly different from that of fish transferred to impoundments of the Muskegon River (p. 10). In the Muskegon River, 91 percent of the total recoveries (1947, 1948, and 1950 data combined) were made during the first year after release, and not one tagged fish was recovered in the impoundments more than 15 months after tagging. In the Inland Waterway, the percentage of the total returns was low (3.7 percent) during the first year after transfer, and transferred walleyes contributed to the fishery over an unbroken span of 10 fishing seasons. The most recent known recovery was on October 25, 1951, 9½ years after release in Black Lake.

In contrast to the marked tendency of walleyes transferred to the Muskegon River impoundments to move downstream, walleyes transferred to the Inland Waterway were more commonly recovered upstream, particularly when they were released in the lower reaches of the Waterway. Of six walleyes released in the Cheboygan River above Cheboygan Dam, four were recaptured far upstream. Among recoveries of fish released in Mullett Lake, the farthest downstream of the lakes in the chain, six had moved to upstream waters, one was caught in Mullett Lake, and one had moved 2 miles downstream in the Cheboygan River and 4 miles upstream in the Black River before being recaptured. Of 11 recoveries of tagged fish in Burt Lake, five were caught in this lake and six were recovered upstream. Of 18 recoveries of tagged fish released in Crooked Lake, 13 were caught there and five had moved out (two upstream and three downstream). Black Lake was an exception, as 8 of 20 recoveries were from downstream waters and one was upstream from the locality of release. Migration of fish from connecting waters into this lake is blocked by a dam in its outlet and no connecting lakes are in the drainage above it.[9]

In 1948, 300 native walleyes were tagged and released in Burt Lake. To date, 50 (16.7 percent) have been recovered (Table 6; Fig. 3). Of these recaptures, 39 were made in Burt Lake, 10 in upstream waters (six in the Sturgeon River, two in the Crooked River, and two in Pickerel Lake), and one downstream from the planting locality (in the Indian River).

The native walleyes thus showed a somewhat greater tendency to remain in Burt Lake than did the walleyes transferred to this water in 1942, from the Cheboygan River below Cheboygan Dam. Most movement that did occur, however, was in an upstream direction, as was true in the earlier experiment with transferred fish.

Females were more vulnerable to anglers than were males among walleyes tagged in Burt Lake in 1948. Although only 78 (26 percent) of the 300 walleyes tagged were females, 14 of 20 (70 percent) of the first-year recoveries were of this sex. Females thus showed a first-year recovery rate of 17.9 percent, whereas this percentage for males was only 2.7 percent. Two additional fe-

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[9] A detailed map showing localities of recovery and release of walleyes transferred to the Inland Waterway in 1942 was given by Eschmeyer (1950, p. 88).

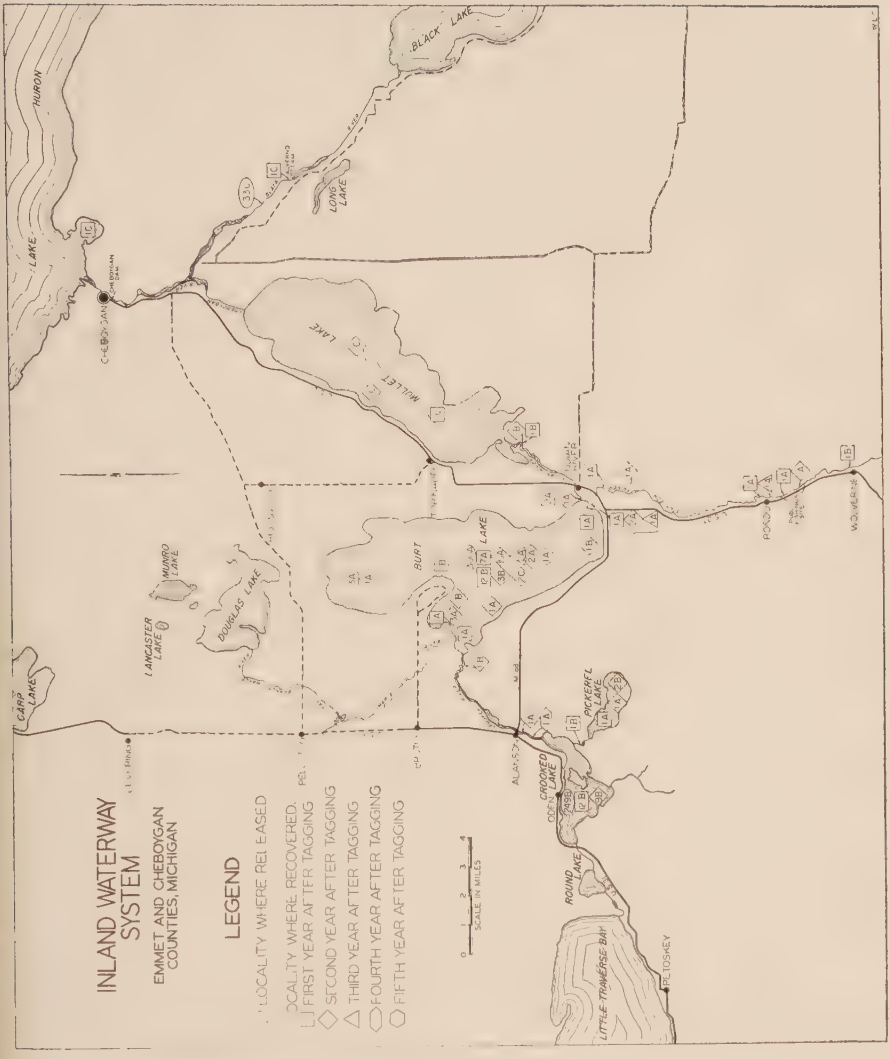
INLAND WATERWAY SYSTEM
EMMET AND CHEBOYGAN COUNTIES, MICHIGAN
LEGEND
LOCALITY WHERE RELEASED
LOCALITY WHERE RECOVERED.
FIRST YEAR AFTER TAGGING
SECOND YEAR AFTER TAGGING
THIRD YEAR AFTER TAGGING
FOURTH YEAR AFTER TAGGING
FIFTH YEAR AFTER TAGGING
SCALE IN MILES
0 1 2 3 4
LAKE HURON
BLACK LAKE
LONG LAKE
MULLET LAKE
BURT LAKE
DOUGLAS LAKE
MUNRO LAKE
LANCASTER LAKE
CARP LAKE
PICKERFL LAKE
CROOKED LAKE
ROUND LAKE
LITTLE TRAVERSE BAY
CHEBOYGAN
CHEBOYGAN DAM
PETOSKEY
ALANSON
ODEN
PONSHEWAING
INDIAN RIVER
WOLVERINE
PELLSTON
1C
33C
1B
1A
3A
2A
7A
12B
249B
9B
2B

Figure 3.—Localities of release and of recovery of native walleyes tagged in the Inland Waterway System, Emmet and Cheboygan counties, Michigan. Places of release are designated as follows: A—Burt Lake (April, 1948); B—Crooked Lake (January-April, 1952); and C—Black River (May, 1952).

males were caught during the second year after tagging; all other recoveries were males. The 50 recoveries during the five-year period following tagging were composed of 34 males (15.3 percent return) and 16 females (20.5 percent).[10]

During the winter and early spring of 1952, 249 native walleyes taken in trap nets set under the ice, were tagged in Crooked Lake. From this group, 28 (11.2 percent) were recovered during the first year after tagging and 18 (7.2 percent) were caught in 1953. Of the 1952 recoveries, 12 were caught near the tagging locality, 13 had moved downsteam to Burt Lake and one to the mouth of the Indian River. One fish had moved upstream to the channel connecting Crooked and Pickerel lakes, whereas another had moved downstream 15 miles to the south end of Burt Lake and then upstream 11 miles in the Sturgeon River, to a point near Wolverine, Michigan. Among the 1953 recoveries from this experiment were nine from Crooked Lake, two from Pickerel Lake, one from the Crooked River, five from Burt Lake, and one from the Indian River.

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[10] A significantly greater rate of return for females than for males was also shown in Lake Gogebic (p. 22), but returns from adult walleyes tagged in the Muskegon River showed no consistent difference between the sexes.

Of 33 walleyes tagged in the Black River, near Alverno Dam, in 1952, three were recovered during the first year after tagging (one near the locality of release, one in Mullett Lake, and one in Lake Huron), and four were recovered during the second year (two in Mullett Lake and two in Burt Lake).

The rate of recovery of walleyes tagged in the Inland Waterway in 1948 and 1952 was markedly higher (with some additional returns still expected) than that of walleyes transferred to these waters in 1942. The extent to which the returns may have been influenced by low fishing pressures during the years of World War II, and increased fishing pressures in recent years, can only be conjectured. The two experiments are in accord in the demonstration of extensive movement throughout the Inland Waterway of both native and transferred fish.

TAGGING EXPERIMENTS IN OTHER MICHIGAN WATERS

The results of six tagging experiments which have been conducted at localities outside the Inland Waterway and the Muskegon River drainage are summarized in Table 7. The largest single study was in Lake Gogebic, where 4,400 walleyes were jaw-tagged in May 1947 during the spawning season. Returns from this lightly fished water amounted to 7.0 percent during the seven years following marking. Recoveries during the first year were only 1.5 percent, despite rather extensive local publicity given the experiment by placards placed at strategic points about the lake, notices in local newspapers, and personal contacts of a creel-census clerk. The recoveries were spread rather evenly over an extended period. Their number was only 12.5 percent less during the fourth fishing season (56 recoveries) than during the first (64). The number of returns has diminished each year since 1950.[11]

Walleyes tagged in Lake Gogebic moved to all portions of the lake between the time of release and recovery, but all returns reported during the first three years after tagging were restricted to the lake. Six fish recovered during later years had left the lake. These recaptures included: three walleyes in 1950 and one in 1951 caught immediately below Bergland Dam, a small dam located in the outlet about 1 mile from the lake; one recovered in 1950 that had wandered about 21 miles downstream and then moved 30 miles upstream in the South Branch of the Ontonagon River; and one walleye recovered in 1952 that had moved downstream to Victoria Reservoir, a distance of about 30 miles.

In Lake Gogebic, as at Burt Lake (p. 20), the rate of return was higher for tagged female walleyes than for males. Although only 20 percent of the 4,383 walleyes for which sex was determined at time of tagging were females, 35 percent of the recoveries during the seven years after tagging were of this sex. The percentage return from 878 females was more than double that from 3,505 males during each of the first three years after tagging, and exceeded the recovery rate for males during the fourth year. The total return for the seven years following tagging was 5.6 percent for males and 11.8 percent for females.

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[11] In exception to this trend, 16 tagged walleyes were recovered during the first 10 months of 1954.

TABLE 7—NUMBER AND PERCENTAGE (IN PARENTHESES) OF TAGGED WALLEYES RECOVERED BY FISHERMEN IN MICHIGAN LAKES, 1939-1953

Locality of release	Date tagged		Number tagged	Year after tagging†								Total
	Month*	Year		1	2	3	4	5	6	7	11‡	
Lake Gogebic......	5	1947	4,400	64 (1.5)	80 (1.8)	47 (1.1)	56 (1.3)	39 (0.9)	17 (0.4)	7 (0.2)	---	310 (7.0)
Lake Gogebic......	4, 5, 6, 7, 8, 9, 10	1940	94	8 (8.5)	2 (2.1)	2 (2.1)	...	...	...	...	...	12 (12.8)
Cadillac Lake......	6	1947	297	10 (3.4)	6 (2.0)	8 (2.7)	3 (1.0)	1 (0.3)	2 (0.7)	2 (0.7)	---	32 (10.8)
East Twin Lake....	7, 8	1939	103	...	6 (5.8)	1 (1.0)	...	...	...	...	3 (2.9)	10 (9.7)
Saginaw Bay, Lake Huron.....	4	1942	198	3 (1.5)	4 (2.0)	...	...	...	...	...	...	7 (3.5)
Hamlin Lake......	3, 4	1949	69	...	2 (2.9)	...	...	...	---	---	---	2 (2.9)
Total.......	...	...	5,161	85 (1.6)	100 (1.9)	58 (1.1)	59 (1.1)	40 (0.8)	19 (0.4)	9 (0.2)	3 (0.1)	373 (7.2)

*Months are numbered consecutively, from March (3) to October (10).

†First year extends from date of tagging through December 31 of that year; subsequent intervals refer to later calendar years. In the body of the table, "..." indicate no recoveries during year, "---" indicate that recoveries could not have been expected because the experiment was not in progress.

‡No recoveries during eighth, ninth, and tenth year after tagging. The 3 fish from East Twin Lake were caught during the months of January and February, 1949 about 9½ years after tagging, but during the eleventh calendar year following tagging (see footnote †).

The rate of recovery from 94 walleyes tagged in 1940 in the outlet of Lake Gogebic, about 1 mile downstream from the lake, was higher than that from fish tagged in 1947. Of 12 recoveries (12.8 percent) made during the first three years following tagging, eight were recaptured in the river or near its source, within about a mile of the tagging locality, and four were recovered in Lake Gogebic. The apparent tendency for the tagged fish to concentrate below Bergland Dam, a popular fishing area, may have contributed to the higher recovery rate.

Of 297 walleyes tagged in Cadillac Lake in June 1947, 32 (10.8 percent) were recovered during the following seven years. Here, as at Lake Gogebic, returns were spread over several fishing seasons and did not exceed 3.4 percent during any single year. The returns diminished markedly, however, after the third year. All fish were recovered in the lake in which they were released.

In East Twin Lake, 103 native walleyes were tagged in July and August 1939. No returns were reported during the remainder of that year, but six fish were recovered by anglers in 1940 and one in 1941. After a lapse of seven years during which no recaptures were reported, three were taken by anglers fishing through the ice in January and February 1949, about 9½ years after tagging.

The release of 198 jaw-tagged native walleyes in Saginaw Bay, Lake Huron, in April 1942 yielded three returns during the first year and four during the second (all near the tagging locality), for a total return of 3.5 percent.

In Hamlin Lake, two recoveries, both during the second fishing season after marking, followed the tagging of 69 walleyes in March and April 1949, after they had been transferred to the lake from a point below the dam in its outlet.

Comparison of Rate of Recovery of Tagged Walleyes in Michigan with that in other Areas

The results of walleye tagging in Michigan are summarized in Table 8, which is based on the data of Tables 2, 6, and 7. Of 11,354 walleyes tagged during the 14-year period, 1939-1952, 1,390 (12.2 percent) had been recovered by December 31, 1953.

The highest rate of return was in the Muskegon River drainage, where recaptures from 5,043 tagged walleyes numbered 850, or 16.9 percent. In lakes and streams of the Inland Waterway, anglers recovered 167 (14.5 percent) of 1,150 walleyes tagged during the period 1942-1952; and in other Michigan waters only 373 (7.2 percent) of 5,161 marked fish were recaptured. A seemingly obvious conclusion from the tagging studies is that only a small percentage of the walleyes in these representative Michigan waters reached anglers' creels; most presumably died of natural causes.

Results of walleye tagging experiments in waters outside Michigan are summarized in Table 9. The highest rate of return that has been reported to date was at Spirit Lake, Iowa, (Rose, 1949) where 28.2 percent of 556 walleyes tagged in 1947 were recaptured during the first year after tagging. Eddy and Surber (1947), apparently revising earlier records by Stoudt (1939), reported a recovery of 22.5 percent from 3,000 walleyes tagged in tributaries of Lake Winnibigoshish, Minnesota. In Blackduck River, Minnesota, Smith, Krefting, and Butler (1952) reported a recovery of 25.1 percent (by sport and commercial fishermen) of 4,697 walleyes tagged in 1949. Patterson (1953) secured a 20.5 percent return from 984 walleyes marked in Escanaba Lake,

Table 8—Number and Percentage (in parentheses) of Tagged Walleyes Recovered by Fishermen in Michigan, 1939–1953

Region where tagged	Years of tagging	Number tagged	Year after tagging*											Total
			1	2	3	4	5	6	7	8	9	10	11	
Muskegon River drainage....	1939–1952	5,043	679 (13.5)	111 (2.2)	33 (0.7)	16 (0.3)	8 (0.2)	†2 (0.0)	†1 (0.0)	. .	. . .	. . .	. . .	850 (16.9)
Inland Waterway.......	1942–1952	1,150	72 (6.3)	52 (4.5)	19 (1.7)	9 (0.8)	6 (0.5)	3 (0.3)	1 (0.1)	2 (0.2)	1 (0.1)	2 (0.2)	. . .	167 (14.5)
Other waters.....	1939–1949	5,161	85 (1.6)	100 (1.9)	58 (1.1)	59 (1.1)	40 (0.8)	19 (0.4)	9 (0.2)	. . .	. . .	. . .	3 (0.1)	373 (7.2)
Total....	. . .	11,354	836 (7.4)	263 (2.3)	110 (1.0)	84 (0.7)	54 (0.5)	24 (0.2)	11 (0.1)	†2 (0.0)	†1 (0.0)	†2 (0.0)	†3 (0.0)	1,390 (12.2)

*First year extends from date of tagging through December 31 of that year; subsequent intervals refer to later calendar years.

†Less than 0.05 percent.

TABLE 9—RATE OF RECOVERY OF TAGGED WALLEYES IN WATERS OUTSIDE MICHIGAN

Water, and reference	Year tagged	Number tagged	Number of years for which recoveries were reported*	Percentage recovered
Little Cut Foot Sioux and Dixon Lakes, Minnesota†..... (Stoudt and Eddy, 1939)	1937–1938	2,983	1–2	16.3
Lake Erie.................. (Doan, 1942)	1938–1940	1,248	1–3	1.8
Norris Reservoir, Tennessee... (Eschmeyer, 1942)	1940	28	1	14.3
Wolf River, Wisconsin........ (Herman, 1947)	1944–1946	3,694	1–3	9.3
Spirit Lake, Iowa............ (Rose, 1949)	1947	556	1	28.2
Norris Reservoir, Tennessee... (Manges, 1950)	1947–1949	427	1–3	17.6
Claytor Lake, Virginia........ (Roseberry, 1951)	1948–1949	130	1	11.5
Blackduck River, Minnesota.. (Smith *et al.*, 1952)	1949	4,697	3	25.1
Tamarack River, Minnesota .. (Smith, *et al.*, 1952)	1950–1951	5,042	1–2	7.8
Escanaba Lake, Wisconsin.... (Patterson, 1953)	1951	984	1	20.5
Richelieu River, Quebec...... (Desrochers, 1953)	1952	2,088	1	24.2

*Recoveries of walleyes from some of the lots of fish tagged were observed for different periods of years following tagging. Detailed data were given in the references cited.

†Many of the recoveries were from Lake Winnibigoshish, a connecting water. This study included an earlier report by Stoudt (1939) and was apparently also referred to by Eddy and Surber (1947), who reported a total return of 22.5 percent during the four years after tagging.

Wisconsin. Of 2,088 tagged walleyes transferred from northern Lake Champlain to Chambly Reservoir, in the Richelieu River, Quebec, 505 (24.2 percent) were recovered within about seven months after tagging (Desrochers, 1953). Returns of tagged walleyes from other waters which have been studied were less than 20 percent (Table 9). Thus, in some waters of other areas, too, a large proportion of the walleyes supposedly available to fishermen are apparently not caught.

THE EFFECT OF JAW TAGS ON GROWTH, CONDITION, AND SURVIVAL

Several investigators (Rose, 1949; Smith, Krefting, and Butler, 1952; and Patterson, 1953) have shown that the presence of jaw tags tends to retard the growth rate of walleyes, although it does not necessarily affect the condition of the marked fish. These findings were corroborated in Michigan.

In Lake Gogebic 37 walleyes were recovered in trap nets October 14–22, 1947, after they had carried jaw tags over a period of approximately five months. Their growth during this period is compared with the average annual increment of untagged fish in the population (from Eschmeyer, 1950) in Table 10.

TABLE 10—GROWTH OF TAGGED WALLEYES RECOVERED AFTER ONE GROWING SEASON, LAKE GOGEBIC, MICHIGAN, 1947

Age when tagged	Sex	Number of fish	Average total length (inches), at time of		Average increment (inches)		Increment of tagged fish (percentage of increment of untagged fish)
			Release	Recovery	Tagged fish	Untagged fish	
IV........	Male	4	14.7	15.8	1.1	1.3	84.6
V.........	Male	10	16.2	16.7	0.5	1.1	45.5
	Female	6	17.4	18.6	1.2	1.6	75.0
VI........	Male	2	17.9	17.9	0.0	0.6	0.0
	Female	4	18.1	18.7	0.6	1.0	60.0
VII.......	Male	2	17.3	18.0	0.7	0.4	175.0
	Female	5	18.3	19.1	0.8	0.9	88.9
VIII......	Female	1	21.0	21.2	0.2	0.6	33.3
IX.......	Male	2	18.8	18.8	0.0	0.3	0.0
	Female	1	20.4	20.5	0.1	0.6	16.7
Total or weighted average	...	37	...	...	...	...	62.9

The ages of the recovered fish ranged from four to nine years and their total lengths from 14.2 to 21.0 inches at the time of tagging. In the analysis it was assumed that the 1947 growing season had been completed at the time of the October collection because 63 of 97 untagged walleyes of these age groups, collected at the same time, had completed growth equal to the average annual increment for fish of their respective age and sex. (In May 1947, 194 walleyes of age groups I to X had not yet formed an annulus.) The average growth increment of tagged walleyes was less than that of unmarked fish in all age groups except VII–group males (Table 10). Although the percentage of the normal increment attained by the tagged fish varied widely, the average of 62.9 for the group suggests a marked retardation of growth as a result of the presence of the tags. The October measurements were not influenced by possible loss of distal portions of the caudal fin resulting from handling and tagging five months earlier since no frayed fins were observed on the tagged fish, and the ratio of standard to total length of the tagged fish (0.839) was similar to that of untagged fish in the population (0.834, based on 373 individuals between the lengths of 14.0 and 21.5 inches).

The presence of No. 3 jaw tags had no apparent effect on the condition (robustness) of the walleyes examined after five months of freedom. The 37 recovered fish had an average K[12] of 1.70; 97 untagged walleyes of the same range in length and age collected at the same time in the same nets had a mean K of 1.66. Walleyes in Lake Gogebic in 1947 were in excellent condition, as indicated by the condition factor, which is among the highest reported to date for fish of this species.

Walleyes commonly showed a loss in total length soon after handling and tagging, due at least in part to the loss of the distal portions of the caudal fin (Fig. 4).[13] Although regeneration of the damaged portions of the fins was completed before the end of the first growing season by tagged walleyes recovered in Lake Gogebic in 1947, regeneration was slower or did not take place among walleyes transferred to the Muskegon River impoundments in 1948. Even untagged transferred walleyes were recognizable to a trained observer throughout the first season after transfer. On most fish the frayed caudal and soft dorsal fins were conspicuous, whereas fish which had regained their loss in length showed a characteristic line of demarcation between the regenerated portions and the remainder of the fin.

The extent and duration of the loss in length of walleyes transferred to Hardy Pond were observed in 1948 when 33 tagged fish were measured from 1 to 4½ months after transfer from the Muskegon River below Newaygo Dam in April. Of this number, 20 were recaptured in trap nets and 13 were caught by anglers and measured by a creel-census clerk. None of the fish showed a gain in length; nine fish had the same length as when tagged; and 24 showed losses ranging from 0.1 to 0.6 inch (Table 11). The loss of length had not been regained by late August, for 11 of 16 measurements made between July 1 and September 3 were made after August 23.[14]

In Norris Reservoir, Tennessee, Eschmeyer and Jones (1941) also found that the lengths of tagged fish recaptured soon after tagging tended to be several millimeters shorter than at the time of tagging.

To compare survival of tagged and untagged walleyes held under identical conditions, 48 walleyes were transferred from the Muskegon River below Newaygo Dam to a 0.9-acre rearing pond, on April 18, 1947. Twenty-four of the fish were unmarked; the remainder were marked with jaw tags—16 with No. 3 strap tags, (eight on the lower jaw and eight on the upper jaw) and eight with large (No. 18) strap tags on the lower jaw. The average total length of the unmarked fish was 20.2 inches (range, 13.7–23.5); the mean length of the tagged fish was 20.3 inches (range, 12.7–23.8). Advanced fry and fingerlings of the white sucker, *Catostomus commersoni commersoni* (Lacépède), were placed in the pond for food, as required.

The numbers of surviving tagged and untagged fish on each of four dates when they were examined are shown in Table 12. On July 22 and November 10, 1947, approximately equal numbers of both lots of fish remained (15

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[12] $K = \dfrac{10^5 W}{L^3}$ where W = weight in grams and L = standard length in millimeters.

[13] Loss in length of walleyes after handling was observed in a hatchery rearing pond, to which 24 tagged fish were transferred, from the Muskegon River below Newaygo Dam, on April 18, 1947. Average increments in total length (inches) on each of four dates when the tagged fish were examined were as follows (number of fish in parentheses): July 22, 1947, −0.2 (21); November 10, 1947, +0.6 (15); June 3, 1948, −0.2 (8); September 3, 1948, +0.3 (6). Increases in average length were shown when a growing season intervened between successive examinations; losses were shown when a growing season did not intervene. These losses may have been due in part to causes other than the loss of the distal portions of the caudal fin, because five of seven walleyes which showed a loss in total length on June 3, 1948, also showed a loss in standard length. (Standard lengths were not measured earlier in the experiment).

[14] The measurements of tagged fish at Hardy Pond in 1948 provided an opportunity to check the length measurements reported by fishermen for 64 tagged walleyes caught in Hardy Pond during the season. Increments reported ranged from +5.2 to —5.6 inches, although two-thirds of the measurements were within about ½ inch of the possible correct length.

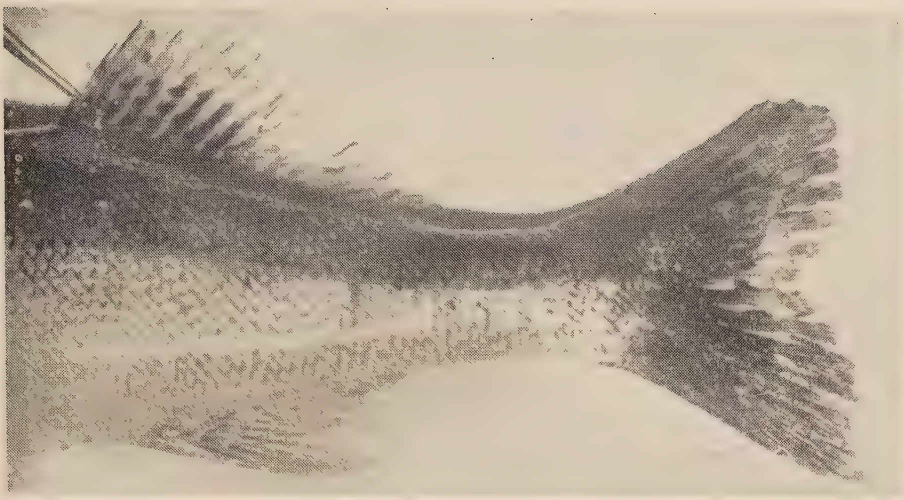

Figure 4.—Soft dorsal and caudal fins of a walleye tagged in Lake Gogebic May 11, 1947, and recovered July 9, 1947, showing fraying presumably resulting from handling. Total length of this fish when tagged—15.2 inches; length when recovered—14.9 inches.

tagged and 16 untagged on the latter date), but by June 3, 1948, only eight tagged fish survived, whereas 12 unmarked fish were still present. Two fish were lost from each lot (tagged and untagged) between June 3 and September 3, 1948, when the survivors numbered six (25.0 percent) tagged and 10 (41.7 percent) untagged fish.

TABLE 11—DISTRIBUTION OF LENGTH INCREMENTS OF TAGGED WALLEYES BETWEEN THE DATE OF RELEASE IN HARDY POND (APRIL 1948) AND RECAPTURE IN TRAP NETS OR BY ANGLERS AT TWO LATER PERIODS

Increment of total length (inches)	Number of fish measured*	
	May 14–June 20	July 1–September 3
0.0	6	3
—0.1	5	2
—0.2	2	4
—0.3	1	3
—0.4	2	3
—0.5	...	1
—0.6	1	...
Average increment	—0.2	—0.2
Number of fish	17	16

*One tagged walleye of this group showed a positive increment in length of 0.7 inch. Since this undoubtedly resulted from an error in measurement, the data are not included.

TABLE 12—SURVIVAL OF TAGGED AND UNTAGGED WALLEYES IN A HATCHERY REARING POND AFTER TRANSFER FROM THE MUSKEGON RIVER BELOW NEWAYGO DAM, APRIL 18, 1947

Date	Tagged fish		Untagged fish	
	Number	Percentage	Number	Percentage
April 18, 1947	24	100.0	24	100.0
July 22, 1947	21	87.5	22	91.7
November 10, 1947	15	62.5	16	66.7
June 3, 1948	8	33.3	12	50.0
September 3, 1948	6	25.0	10	41.7

The relatively higher loss of marked than of unmarked walleyes during the first winter following transfer, *i.e.* between November 10 and June 3, suggests that tags may have had some influence on mortality (although the difference between the two lots of fish was not statistically significant in this limited experiment). There is reason to believe, however, that the large size of the tags used on some of the fish may have been the principal cause of this greater loss. Four of the seven marked fish which died during this period had been tagged with the large (No. 18) tag. At the time of the November 10, 1947, examination, these four fish were in extremely poor condition (average *K*, 1.01; range 0.92–1.06) in comparison with the other survivors. The average condition factor on this date of nine fish with small (No. 3) tags on the upper or lower jaw was 1.47 (range, 1.32–1.71) and the mean *K* of the 16 unmarked fish was 1.42. This demonstration of the serious physical effect of the large jaw tag on fish of this size range (smaller than most fish on which this tag ordinarily was used) limits the usefulness of the experiment in assaying the general effect of jaw-tagging (with tags of suitable size) on mortality.

SUMMARY

Of 2,783 walleyes marked with strap tags attached to the gill covers and released at five localities during the years 1929-1932, only 37 (1.3 percent) were subsequently recovered by anglers. No fish were recovered more than 6½ months after tagging.

A total of 3,371 jaw-tagged walleyes were transferred to upstream impoundments from the Muskegon River below Newaygo Dam in 1947, 1948, and 1950. Of these, 617 (18.3 percent) were recovered by fishermen. Most (91 percent) of the recoveries were made during the first year after transfer. The transferred fish showed a marked proclivity to move downstream past power dams. The total number of passages across individual dams was 352, and three tagged walleyes successfully negotiated five of the structures, which were from 17 to 100 feet high. Of the walleyes stocked in the impoundments 18 percent had regained direct access to Lake Michigan by the time of recapture.

Of 765 walleyes tagged and released in the Muskegon River below Newaygo Dam in 1948 and 1950, 96 (12.5 percent) had been recovered by the end of 1953. A total of 38 walleyes released below Newaygo Dam and 45 fish released in the upstream impoundments were recaptured in Lake Michigan. Fourteen walleyes had traveled more than 100 miles between the date of release and recapture and one had moved 175 miles. Lake Michigan recoveries were scattered along the east shore from as far south as Porter Beach, Indiana, to as far north as Good Harbor Bay, points which are about 250 miles apart.

Of 395 native walleyes marked in 1948 and 1952 in Hardy Pond, the largest of the Muskegon River impoundments, 40 had been recovered by the end of 1953—8 of them in downstream waters, after having passed one or more of the power dams.

Returns from 568 jaw-tagged walleyes transferred in 1942 from the Cheboygan River below Cheboygan Dam to lakes and streams of the Inland Waterway numbered 64 (11.3 percent). The pattern of recoveries indicated extensive movement by the transferred fish (primarily upstream). Recaptures were spread over an unbroken span of 10 fishing seasons. Two walleyes were recovered more than nine years after tagging.

A total of 103 (17.7 percent) of 582 native walleyes tagged in the Inland Waterway in 1948 and 1952 have been recovered to date. Movement of the fish among the lakes and streams of the Waterway was about as extensive as that of walleyes introduced from the lower Cheboygan River in the 1942 experiment.

Total returns from 5,161 walleyes tagged in the years 1939-1949 in five other localities in Michigan have equaled 373 (7.2 percent). The return to date from the grand total of 11,351 walleyes that have been jaw-tagged in Michigan during the period 1939-1952 is only 12.2 percent. This small return suggests that a large proportion of the walleyes in these representative waters never reach anglers' creels.

Growth was found to be retarded by the presence of jaw tags. The length increment of 37 Lake Gogebic walleyes recovered in 1947 after bearing tags during one growing season averaged less than two-thirds that of untagged fish. The condition of the fish was not affected by the tags.

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AGE AND LENGTH COMPOSITION OF THE SARDINE CATCH OFF THE PACIFIC COAST OF THE UNITED STATES AND MEXICO IN 1954-55[1]

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This report on age and length composition of the catch of sardines *(Sardinops caerulea)* off the Pacific Coast of North America is the ninth of a series which gives similar data from 1941-42 to the present season (Felin et al., 1954).

During the 1954-55 season, 65,918 tons were landed in the San Pedro region; this included fish landed at Santa Barbara, Port Hueneme, Santa Monica, Los Angeles-Long Beach Harbor, and Newport. Fish from some of these points were trucked to Monterey, Moss Landing, and San Francisco for processing during October, November, and December. At San Diego 510 tons were landed and trucked to the Los Angeles area for processing. In August and September, 830 tons were landed at Avila and trucked to Monterey and Moss Landing for processing. No fish were landed at Monterey, Moss Landing, or San Francisco.

The fishing season at San Pedro and San Diego, as for the several preceding years, extended from October 1st to February 1st; that in the Monterey region extended from August 1st to January 15th. For Ensenada, Baja California, where fishing is carried on throughout the year, data for a period approximating the California canning season only were used—in this case, July 30th to January 7th.

Sampling was carried on, as described for recent preceding seasons, at Monterey, San Pedro, San Diego, and Ensenada. Sampling and age determinations were continued by personnel of the California Department of Fish and Game and the U. S. Fish and Wildlife Service.

Tables 1-5 show, by sex and area of catch, the length-frequency distributions of sardines of each year class as taken in the 1954-55 random scale samples.

Table 6 gives calendar dates for the lunar months included in Table 7.

Table 7 gives total tonnages and numbers of fish of each age caught in each region, estimated in the same manner as described for preceding seasons.

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[1] Submitted for publication April, 1955.

Table 8 gives, by sex and region of catch, the mean length and standard error of the mean for each year class sampled in the 1954-55 season. These are based on the random scale samples.

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TABLE 1

Length Composition of the 1954, 1953, and 1952 Year Classes in 1954-55

Standard length mm.	1954 year class, age 0 San Pedro	1953 year class, age 1									1952 year class, age 2																	
		San Pedro			Ensenada			Grand total			Monterey			San Pedro			San Diego			California total			Ensenada			Grand total		
	T	M	F	T	M	F	T	M	F	T	M	F	T	M	F	T	M	F	T	M	F	T	M	F	T	M	F	T
134	1																											
136	3																											
138	5																											
140	3																											
142	10																											
144	4																											
146	3																											
148	1																											
186																												
188														1		1				1		1				1		1
190																							1		1	1		1
192			1	1					1	1				5		5	1		1	6		6	2		2	8		8
194														9	4	13		1	1	9	5	14		1	1	9	6	15
196						1	1		1	1				11	6	17	1		1	12	6	18	2	2	4	14	8	22
198			2	2					2	2				13	2	15	1	1	2	14	3	17	3	3	6	17	6	23
200														19	8	27	2		2	21	8	29		2	2	21	10	31
202														16	18	34	2	2	4	18	20	38	2	2	4	20	22	42
204														14	11	25		1	1	14	12	26	1	2	3	15	14	29
206														9	22	31				9	22	31				9	22	31
208														3	16	19				3	16	19		1	1	3	17	20
210											1		1	3	6	9				4	6	10				4	6	10
212														2	7	9				2	7	9		1	1	2	8	10
214														1	2	3		1	1	1	3	4				1	3	4
216														1	1	2				1	1	2				1	1	2
218														1	2	3				1	2	3				1	2	3
220															1	1					1	1					1	1
222																												
224																												
226																							1		1	1		1
Totals	30*		3	3		1	1		4	4	1		1	108	106	214	7	6	13	116	112	228	12	14	26	128	126	254

* Includes 30 young sardines of undetermined sex.

TABLE 2

Length Composition of the 1951 Year Class in 1954-55

Standard length mm.	1951 year class, age 3																	
	Monterey			San Pedro			San Diego			California total			Ensenada			Grand total		
	M	F	T	M	F	T	M	F	T	M	F	T	M	F	T	M	F	T
186				1		1				1		1				1		1
188				2		2				2		2				2		2
190				3		3				3		3				3		3
192				4	2	6				4	2	6				4	2	6
194				11	3	14	1		1	12	3	15		1	1	12	4	16
196				14	2	16	1		1	15	2	17	1		1	16	2	18
198				10	4	14	1		1	11	4	15	3	4	7	14	8	22
200				17	11	28				17	11	28	1		1	18	11	29
202		1	1	16	13	29				16	14	30	1	3	4	17	17	34
204				8	8	16				8	8	16				8	8	16
206				11	17	28	2	1	3	13	18	31	3	1	4	16	19	35
208	1	2	3	7	12	19	1		1	9	14	23		1	1	9	15	24
210				6	10	16				6	10	16	1	1	2	7	11	18
212	1	1	2	7	8	15		1	1	8	10	18	1	1	2	9	11	20
214		2	2	5	3	8	1		1	6	5	11				6	5	11
216		1	1	2	5	7				2	6	8		1	1	2	7	9
218		1	1	1	7	8		1	1	1	9	10				1	9	10
220				2	6	8		1	1	2	7	9				2	7	9
222		1	1	1	2	3		1	1	1	4	5				1	4	5
224					1	1					1	1					1	1
226					1	1					1	1		1	1		2	2
Totals	2	9	11	128	115	243	7	5	12	137	129	266	11	14	25	148	143	291

TABLE 3

Length Composition of the 1950 Year Class in 1954-55

Standard length mm.	1950 year class, age 4																	
	Monterey			San Pedro			San Diego			California total			Ensenada			Grand total		
	M	F	T	M	F	T	M	F	T	M	F	T	M	F	T	M	F	T
190				1		1				1		1				1		1
192																		
194				2		2				2		2				2		2
196				1		1				1		1				1		1
198				2		2		1	1	2	1	3				2	1	3
200				2	1	3				2	1	3				2	1	3
202					2	2					2	2					2	2
204				3	1	4				3	1	4		1	1	3	2	5
206				3	1	4				3	1	4	1		1	4	1	5
208				4	1	5				4	1	5	1		1	5	1	6
210				6	1	7				6	1	7	1	1	2	7	2	9
212	2	1	3	2	4	6				4	5	9	1		1	5	5	10
214				5	3	8				5	3	8	2		2	7	3	10
216	3		3	2	2	4				5	2	7	1		1	6	2	8
218				3	5	8				3	5	8	1		1	4	5	9
220				4	5	9				4	5	9				4	5	9
222		1	1	1	2	3				1	3	4				1	3	4
224					4	4					4	4		1	1		5	5
226					4	4					4	4					4	4
228					1	1					1	1					1	1
230				1	1	2				1	1	2				1	1	2
232														1	1		1	1
234																		
236																		
238					1	1					1	1					1	1
240																		
Totals	5	2	7	42	39	81		1	1	47	42	89	8	4	12	55	46	101

TABLE 4

Length Composition of the 1949 Year Class in 1954-55

Standard length mm.	1949 year class, age 5																	
	Monterey			San Pedro			San Diego			California total			Ensenada			Grand total		
	M	F	T	M	F	T	M	F	T	M	F	T	M	F	T	M	F	T
190																		
192																		
194																		
196				1		1				1		1				1		1
198																		
200				1		1				1		1		1	1	1	1	2
202				1		1				1		1				1		1
204				1		1				1		1				1		1
206				2		2				2		2				2		2
208	1		1	2		2				3		3				3		3
210				4		4				4		4				4		4
212	1	1	2	3	2	5				4	3	7	1	1	2	5	4	9
214		1	1	4	1	5				4	2	6	1		1	5	2	7
216				1	2	3				1	2	3	1	2	3	2	4	6
218				2		2				2		2		1	1	2	1	3
220				1	2	3		1	1	1	3	4	1	1	2	2	4	6
222				2	1	3		1	1	2	2	4		1	1	2	3	5
224					1	1					1	1	1		1	1	1	2
226		1	1		1	1					2	2					2	2
228					1	1					1	1					1	1
230				1	1	2				1	1	2				1	1	2
244				1		1				1		1				1		1
258					1	1					1	1					1	1
Totals	2	3	5	27	13	40		2	2	29	18	47	5	7	12	34	25	59

TABLE 5

Length Composition of the 1948 and 1947 Year Classes in 1954-55

Standard length mm.	1948 year class, age 6																		1947 year class, age 7								
	Monterey			San Pedro			San Diego			California total			Ensenada			Grand total			San Pedro			Ensenada			Grand total		
	M	F	T	M	F	T	M	F	T	M	F	T	M	F	T	M	F	T	M	F	T	M	F	T	M	F	T
198				2	1	3				2	1	3				2	1	3									
200				1		1				1		1				1		1									
202				4		4				4		4		1	1	4	1	5									
204					1	1					1	1					1	1									
206				1		1				1		1				1		1									
208				7	2	9				7	2	9				7	2	9				1		1	1		1
210	1		1	3	3	6				4	3	7				4	3	7	1		1				1		1
212	1		1	8	3	11				9	3	12	1		1	10	3	13		1	1					1	1
214				3	4	7				3	4	7	1	1	2	4	5	9	1		1				1		1
216	2		2	5	4	9				7	4	11	1	1	2	8	5	13	1		1				1		1
218		1	1	8	3	11		2	2	8	6	14		2	2	8	8	16				1		1	1		1
220				4	9	13				4	9	13				4	9	13	2		2				2		2
222				2	1	3				2	1	3	1	1	2	3	2	5		1	1					1	1
224				2	4	6				2	4	6				2	4	6	1		1				1		1
226					1	1					1	1					1	1		1	1					1	1
228					1	1					1	1		1	1		2	2									
230																											
232																											
234					1	1					1	1					1	1									
236					1	1					1	1					1	1									
Totals	4	1	5	50	39	89		2	2	54	42	96	4	7	11	58	49	107	6	3	9	2		2	8	3	11

TABLE 6

Calendar Dates of Lunar Months for the 1954-55 Season

"July"	July 15-August 13
"August"	August 14-September 11
"September"	September 12-October 11
"October"	October 12-November 9
"November"	November 10-December 9
"December"	December 10-January 7
"January"	January 8-February 7

TABLE 7

Age (Year Class) Composition of the Sardine Catch in the 1954-55 Season (Numbers of fish are given in thousands, i.e., 000 omitted)

	Catch		Number of fish by age (year class)							
	Tons	Nos.	0	1	2	3	4	5	6	7
			1954	1953	1952	1951	1950	1949	1948	1947
Monterey										
"July"[1]	29	181	--	--	6	71	42	33	29	--
"August"	579	3,642	--	--	121	1,433	850	655	583	--
"September"	220	1,375	--	--	46	541	321	247	220	--
"October"	1	5	--	--	--	2	1	1	1	--
"November"	1	4	--	--	--	1	1	1	1	--
Totals Monterey	830	5,207	--	--	173	2,048	1,215	937	834	--
San Pedro										
"September"[2]	4,110	30,473	--	--	8,229	10,208	4,723	3,961	2,895	457
"October"	35,026	270,390	--	--	91,067	101,235	30,716	16,656	29,202	1,514
"November"	22,296	179,184	--	2,294	61,209	68,663	17,202	11,754	15,625	2,437
"December"	4,309	34,065	--	--	11,947	11,173	3,134	1,455	5,859	497
"January"	177	3,766	3,766	--	--	--	--	--	--	--
Totals San Pedro	65,918	517,878	3,766	2,294	172,452	191,279	55,775	33,826	53,581	4,905
San Diego[3]										
"October"	42	326	--	--	110	122	37	20	35	2
"November"	267	2,047	--	26	700	785	196	134	178	28
"December"	201	1,610	--	--	565	528	148	69	277	23
Totals San Diego	510	3,983	--	26	1,375	1,435	381	223	490	53
Totals California	67,258	527,068	3,766	2,320	174,000	194,762	57,371	34,986	54,905	4,958
Ensenada[4]										
"July"[1]	865	6,539	--	--	2,747	2,223	--	1,569	--	--
"August"	1,394	10,541	--	--	3,560	2,328	547	1,916	2,190	--
"September"	993	7,510	--	484	2,907	--	2,666	969	484	--
"October"	1,112	8,407	--	--	2,018	2,690	2,354	336	1,009	--
"November"	3,664	27,699	--	--	6,833	13,110	4,246	1,108	1,848	554
"December"	679	5,133	--	--	1,266	2,430	787	205	342	103
Totals Baja California	8,707	65,829	--	484	19,331	22,781	10,600	6,103	5,873	657
Grand totals	75,965	592,897	3,766	2,804	193,331	217,543	67,971	41,089	60,778	5,615

[1] Includes deliveries August 1-13 only.
[2] Includes deliveries October 1-11 only.
[3] Numbers of fish in the San Diego catch were prorated at the same ratio as the San Pedro catch for the comparable months.
[4] Numbers of fish were prorated according to the average weight of fish taken November 3-23.

TABLE 8

Number of Fish, Mean Length, and Standard Error of the Mean for Each Year Class in the 1954-55 Season, by Region of Catch

Year Class	Monterey			San Pedro			San Diego			Ensenada		
	No.	M.	S.E.	No.	M.	S.E.	No.	M.	S.E.	No.	M.	S.E.
1954												
Male	--	--	--	--	--	--	--	--	--	--	--	--
Female	--	--	--	--	--	--	--	--	--	--	--	--
Total	--	--	--	30	141	4.84	--	--	--	--	--	--
1953												
Male	--	--	--	0	--	--	--	--	--	0	--	--
Female	--	--	--	3	196	2.00	--	--	--	1	--	--
Total	--	--	--	3	196	2.00	--	--	--	1	--	--
1952												
Male	1	--	--	108	201	0.52	7	199	1.36	12	200	2.70
Female	0	--	--	106	205	0.51	6	202	2.76	14	201	1.32
Total	1	--	--	214	203	0.39	13	200	1.50	26	200	1.41
1951												
Male	2	--	--	128	202	0.65	7	203	3.02	11	203	1.63
Female	9	213	2.00	115	208	0.69	5	216	2.92	14	205	2.34
Total	11	212	1.67	243	205	0.50	12	208	2.68	25	204	1.48
1950												
Male	5	214	0.98	42	210	1.33	0	--	--	8	212	1.44
Female	2	--	--	39	218	1.33	1	--	--	4	218	6.40
Total	7	215	1.37	81	213	1.04	1	--	--	12	214	2.26
1949												
Male	2	--	--	27	213	1.84	0	--	--	5	217	2.16
Female	3	217	4.38	13	223	3.34	2	--	--	7	215	2.76
Total	5	214	3.06	40	216	1.79	2	--	--	12	216	1.80
1948												
Male	4	214	1.50	50	213	0.95	0	--	--	4	216	2.16
Female	1	--	--	39	217	1.19	2	--	--	7	217	3.02
Total	5	214	1.47	89	215	0.78	2	--	--	11	217	2.00
1947												
Male	--	--	--	6	217	2.04	--	--	--	2	--	--
Female	--	--	--	3	220	4.16	--	--	--	0	--	--
Total	--	--	--	9	218	1.84	--	--	--	2	--	--

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JAPANESE HIGH-SEAS MOTHERSHIP-TYPE DRIFT GILL-NET SALMON FISHERY--1954

By Francis M. Fukuhara*

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BACKGROUND

Japanese salmon fishery interests in 1954 resumed their third year of operation in the North Pacific Ocean since the signing of the Tripartite Fishery Treaty (May

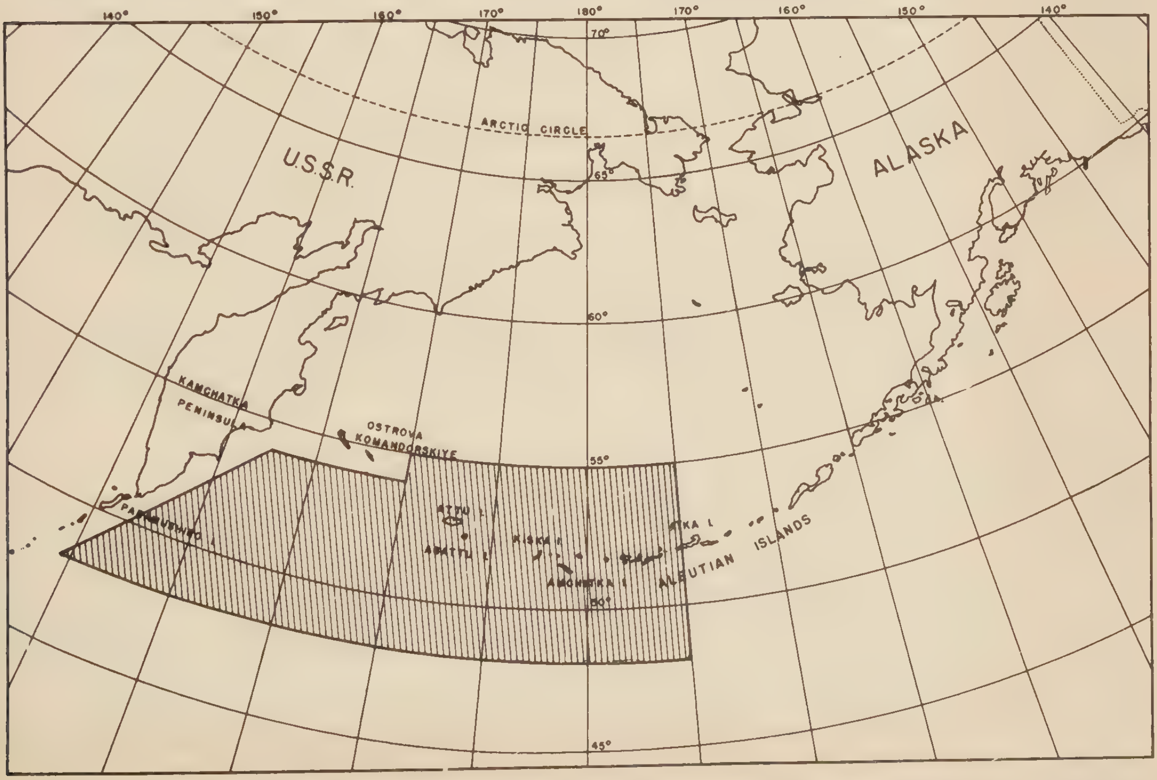
140°
150°
160°
170°
180°
170°
160°
150°
140°
70°
ARCTIC CIRCLE
U.S.S.R.
ALASKA
65°
60°
KAMCHATKA PENINSULA
OSTROVA KOMANDORSKIYE
55°
PARAMUSHIRO I.
ATTU I.
AGATTU I.
KISKA I.
ATKA I.
AMCHITKA I.
ALEUTIAN ISLANDS
50°
45°

Fig. 1 - Chart of the Bering Sea and North Pacific Ocean. Shaded portion shows fishing area authorized by the Japanese Fishery Agency for the 1954 salmon-fishing fleets.

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1952). Prior to departure of the 1952 expedition the Japanese Fishery Agency extended an invitation to the U. S. Fish and Wildlife Service to place a biologist aboard one of the motherships to accompany the fleet during its fishing operations in the offshore waters of the Aleutian Islands and Kamchatka. The activities of that expedition were described by Fukuhara (1953). A similar invitation was extended by the Japanese Fishery Agency to the Service in 1954. In response to this invitation the author was assigned to accompany the Japanese fleet during the 1954 high-seas salmon-fishing season.

The following is a narrative account of the activities of the 1954 salmon fleet.

Transportation to the Japanese fleet was provided by the *U.S. C.G.C. Clover*. Between June 20 and July 9 the writer was aboard the S. S. *Einin Maru*, mothership of the Taiyo Fishing Co., Ltd., and from July 10 to August 23 aboard the M.S. *Miyajima Maru*, mothership of the Nippon Suisan Co., Ltd. The ships' logs, catch data, and the fishing logs of these two fleets were made accessible to the author. These courtesies, extended by Mr. S. Mori and Mr. T. Ito, fleet managers of the Taiyo and Nippon Suisan fleets, respectively, are gratefully acknowledged.

THE FISHING FLEETS

Seven fleets participated in the 1954 high-seas salmon fishery. Descriptions and facilities of all motherships and accompanying catcher boats appear in a Japanese fishery periodical (Anonymous 1954).

Table 1 - Facilities of Motherships

Name	Facilities for:	
	Refrigeration	Canning
Einin Maru	23 compartments	2 lines
Meisei Maru	14 "	-
Kyoho Maru	-	2 lines
Miyajima Maru . .	40 "	1 line
Ginyo Maru.	9 "	-
Kyodo Maru No. 3 .	15 "	-
Saipan Maru	3 tons	-

All motherships were equipped with radio direction finder, Loran, radar, and gyrocompass. Position fixes of motherships were determined by sun sights and by Loran.

The catcher boats of the fleets were coastal trawlers modified for gill-net fishing. Each boat was equipped with a free-wheeling roller on the stern. The catchers ranged in size from 50 to 75 net tons and were driven by 160 to 250 hp. Diesel engines. Maximum speed of catcher boats was 5 to 7.5 knots. Each was equipped with a 50-watt transmitter and in addition carried a radio direction finder. Catcher boats carried crews of 15 to 20 men.

Table 2 - Mothership Descriptions

Name	Gross Tonnage	Length in Meters	hp.	Speed
Einin Maru	7,456	129.9	2,200	11.0 knots
Meisei Maru.	5,603	-	2,100	-
Kyoho Maru	6,900	-	2,100	-
Miyajima Maru	8,964	151.3	5,500	17.0 knots
Ginyo Maru	3,542	96.2	1,800	-
Kyodo Maru No. 3 . .	2,313	85.8	1,700	-
Saipan Maru	3,778	-	900	11.5 knots

The exploratory boats were in some cases slightly larger than the catcher boats; a few exploratory boats were of about 100 net tons. However, these too were trawlers and equipped with a roller on the stern. Exploratory boats carried crews of 18 to 22 men.

The positions of catcher boats were calculated relative to the position of the mothership. Their bearings were established by the radio direction finder from the mothership. The distance of a catcher boat from the mothership was computed from the cruising speed of the catcher boat and the number of hours run from the mothership (cruising speed times hours under way). Due to their greater range of operation, the exploratory boats used sun sights to establish positions.

Table 3 - Number of Catcher Boats by Fleet

Name	No. of Catchers	No. of Scout Boats	Total
Einin Maru	32	6	38
Meisei Maru . . .	28	6	34
Kyoho Maru	19	4	23
Miyajima Maru . .	33	6	39
Ginyo Maru	20	4	24
Kyodo Maru No. 3 .	14	4	18
Saipan Maru	14	4	18
Total	160	34	194

FISHING SEASON

Exploratory boats of all fleets were fishing on the grounds early in May, in advance of the main fleets; however the first motherships to arrive on the fishing grounds commenced fishing operations on May 15, with later fleets commencing operations on May 20.

FISHING AREA AND REGULATIONS PERTINENT TO FISHING

The 1954 mothership-type salmon-fishing operation was limited to an area within a line joining the following points: 55° 00' N., 175° 00' W.; 55° 00' N., 170° 00' E.; 54° 00' N., 170° 00' E.; 54° 00' N.; 162° 30' E.; 48° 00' N., 154° 30' E.; 48° 00' N., 175° 00' W. (fig. 1).

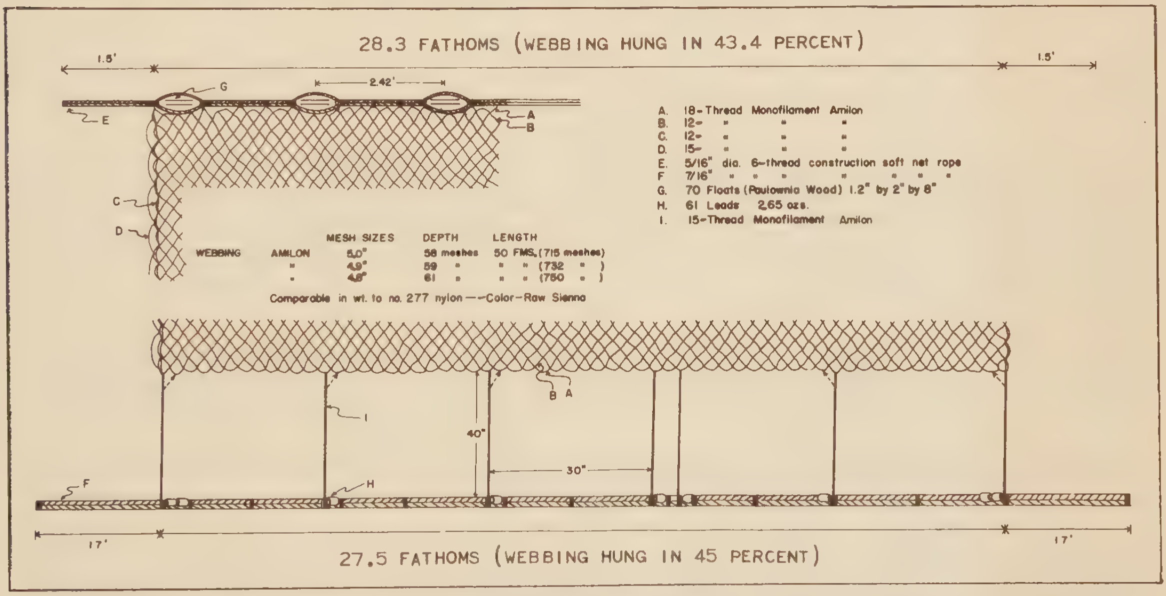

28.3 FATHOMS (WEBBING HUNG IN 43.4 PERCENT)
1.5'
1.5'
2.42'
G
E
A
B
C
D
A. 18-Thread Monofilament Amilon
B. 12- " " "
C. 12- " " "
D. 15- " " "
E. 5/16" dia. 6-thread construction soft net rope
F 7/16" " " " " " " "
G. 70 Floats (Paulownia Wood) 1.2" by 2" by 8"
H. 61 Leads 2.65 ozs.
I. 15-Thread Monofilament Amilon
MESH SIZES DEPTH LENGTH
WEBBING AMILON 5.0" 58 meshes 50 FMS. (715 meshes)
" 4.9" 59 " " " (732 ")
" 4.8" 61 " " " (750 ")
Comparable in wt. to no. 277 nylon -- Color-Raw Sienna
B A
I
40"
30"
F
H
17'
17'
27.5 FATHOMS (WEBBING HUNG IN 45 PERCENT)

Fig. 2 - Details of a "tan" of gill net of the type used by the Nippon Suisan Co. Ltd. fleet. Webbing in net is "Amilon," a synthetic product similar to nylon but with less stretch factor.

All motherships were required to remain at least 50 miles from the boundary of the authorized fishing area and 50 miles away from any of the Aleutian Islands included within the area. Catcher boats were required to remain at least 3 miles from the islands. Five inspection vessels of the Japanese Fishery Agency constantly patrolled the fleets to enforce these regulations. In addition, all catcher boats were required to return to the mothership daily. Because of their limited speed, catcher boats were limited to within a 50-mile radius of the motherships. A Fishery

Agency inspector was assigned to each mothership and among his other duties he checked in all catchers daily. The Fishery Agency inspectors aboard the motherships also received carbon copies of the daily catch by species and by catcher boat, and catcher-boat positions. These data were coded and transmitted to the Chief Inspection vessel every evening.

Fishing operations commenced in the eastern portion of the authorized fishing area and with the advance in season the movement of the fleets was westward. By mid-July all fleets were westward of 160° E. longitude (about 300 miles south of Bering Island in the Kommandorskii group).

SOURCES OF DATA

CATCH DATA: The daily catch by species for the entire fishing season from all the fleets was obtained from the Taiyo Fishing Co., Ltd. As previously stated, daily catch statistics from all motherships were requested by the Japanese Fishery Agency. Related data, such as noon position and numbers of "tan" (units of gill net) set by each catcher boat, were also compiled by the Chief Inspector of the salmon fleet. These data were transmitted to Japan where the information was made available to the companies engaged in the fishery. The companies in turn relayed the information to their motherships on the fishing grounds. Thus the noon position and performance of all fleets for any particular day was common knowledge to all motherships on the following day.

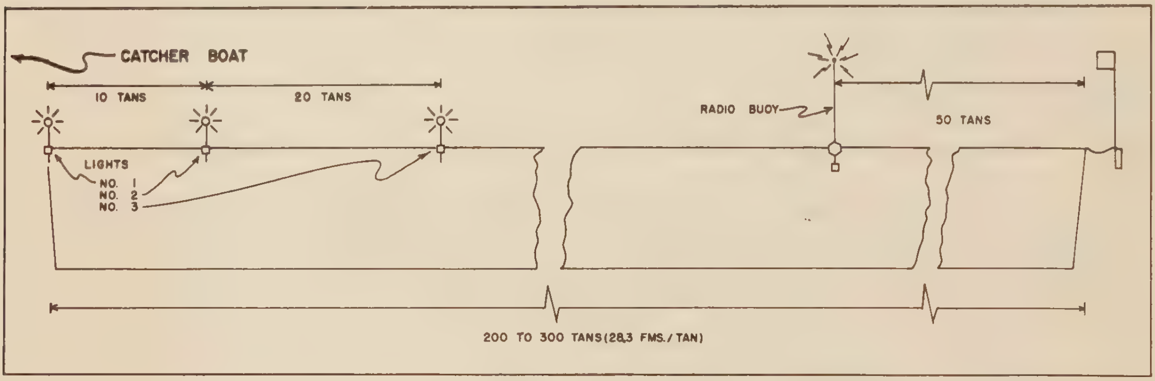


Fig. 3 - Sketch of drift gill-net set.

Catch data for the Einin Maru fleet from June 20 to July 6 was obtained from the Japanese Fishery Agency Inspector assigned to that ship. Catch data for the Miyajima Maru fleet from July 10 to August 17 was obtained from the ship's office.

Species identification and enumeration was done once aboard the catcher boat by the fishermen; a second count was made by sorters aboard the motherships before final figures were entered in the ships' records.

HYDROGRAPHIC OBSERVATIONS: The following data were obtained from the fishing logs of the Einin Maru and Miyajima Maru:

1. Einin Maru (June 20 to July 6)

    (a) Daily catcher boat positions.

    (b) Surface water temperatures taken daily by all catcher boats at position of set.

2. Miyajima Maru (May 16 to August 17)

   (a) Daily catcher boat positions.

   (b) Surface water temperatures taken daily by all catcher boats at position of set.

   (c) Water color (Forel Scale) taken daily by catchers.

   (d) Secchi disk visibility taken daily by catchers.

   (e) Subsurface temperatures to 60 meters taken by exploratory boats only.

Surface water temperatures were taken by all catcher boats generally while under way. All thermometers used by catchers of the Nippon Suisan fleet were calibrated for error by a meteorological agency in Japan. Errors in the instruments for the temperature ranges encountered in the North Pacific during the fishing season were less than 0.1° C. A printed manual was issued with each thermometer to standardize methods of taking temperatures and reading the thermometer.

Table 4 - Average Water Transparency, Water Color, and Surface Water Temperature Recorded by the Miyajima Maru Fleet, May 14 to August 5

Date	Water Transp. 1/	Water Color 2/	Surface Water Temp. °C.
May 14	13.1	4.3	3.6
15	13.0	4.1	3.7
16	12.8	3.9	3.6
17	14.6	4.0	3.6
18	15.0	4.2	3.9
19	14.9	4.4	3.7
20	14.9	4.4	3.8
21	14.8	4.3	3.8
22	14.5	4.4	3.8
23	14.4	4.2	3.7
25	14.6	4.4	3.6
29	15.1	4.3	3.3
30	14.9	4.2	3.3
31	15.2	4.4	3.4
June 1	14.8	4.2	3.3
4	14.8	4.3	3.3
5	15.1	4.3	3.4
7	15.0	4.3	3.6
8	15.2	4.4	3.4
9	15.1	4.3	4.0
10	14.9	4.2	4.0
11	14.7	4.2	3.6
12	14.7	4.3	3.5
13	14.3	4.3	3.7
14	14.4		3.8
15	14.7	4.3	4.4
16	14.6	4.2	4.4
17	14.4	4.4	4.5
18	13.4	4.6	4.6
19	13.1	4.5	4.6
20	13.4	4.4	4.7
21	13.2	4.7	5.1
22	13.2	4.3	5.7
23	13.2	4.4	5.9
24	13.2	4.1	6.1
25	13.3	4.3	6.0
26	12.8	4.4	5.8
27	12.8	4.6	5.6
28	12.3	4.5	5.3
June 29	11.9	4.4	5.5
30	12.2	4.6	5.4
July 1	11.2	4.8	5.2
2	12.0	4.7	5.3
3	11.2	4.8	5.1
4	11.5	4.7	5.3
5	11.9	4.7	5.4
6	11.5	4.6	5.6
7	11.4	4.4	5.4
8	11.2	4.7	5.7
9	10.8	4.5	5.9
10	10.5	4.7	5.9
11	11.2	4.5	6.4
12	10.4	4.7	6.1
13	10.6	4.8	6.0
14	11.1	4.5	6.2
15	11.4	5.4	6.9
16	9.8	5.4	7.3
17	8.8	5.7	7.8
18	7.6	6.2	8.0
19	7.3	6.1	8.8
20	6.7	6.1	8.4
21	9.3	5.2	7.8
22	9.1	5.1	8.0
23	9.2	5.1	7.9
24	9.1	5.2	8.2
25	8.9	5.3	8.6
26	9.1	5.5	8.7
27	9.3	5.1	8.4
28	9.2	5.4	8.2
29	8.8	5.5	8.3
30	8.1	5.4	8.4
31	8.4	5.7	9.7
Aug. 1	8.1	5.8	9.9
2	6.5	6.0	10.5
3	6.9	5.8	10.6
4	9.0	5.3	10.5
5	7.3	5.8	10.5

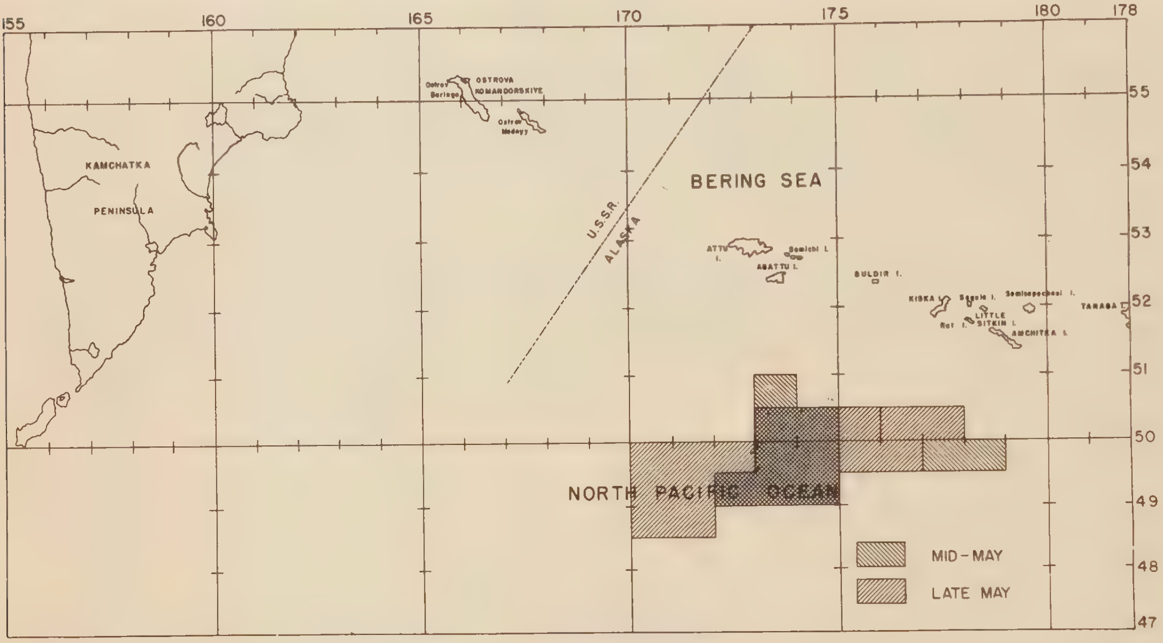
1/ Limit of Secchi-disc visibility in meters.

2/ On the Forel scale.

Color standards were carried by all catcher and exploratory boats of the fleet. These color standards were used in rating the water color on the Forel scale. The Secchi discs used by the Nippon Suisan fleet were all white and 30 cm. in diameter. The exploratory boats of this fleet carried electric thermometers with which surface water and subsurface temperatures were obtained.

FISHING OPERATIONS, METHODS, AND GEAR

MOTHERSHIP MOVEMENT: In a mothership-type fishery the catcher boats are entirely dependent on motherships for fuel, rations, and processing of catch. Furthermore, the cruising range of the catchers was restricted, as stated previously, for they were required to return to the mothership daily except when circumstances (e.g. net caught in screw) made this impossible. In view of these limitations, the success of catcher boats in catching salmon depended almost entirely upon the ability and judgment of the fishing experts whose job it was to situate the mothership in areas of salmon abundance.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OSTROVA KOMANDORSKIYE
Ostrov Mednyy
BERING SEA
U.S.S.R.
ALASKA
ATTU I.
Semichi I.
AGATTU I.
BULDIR I.
KISKA I.
Segula I.
Semisopochnoi I.
LITTLE SITKIN I.
Rat I.
AMCHITKA I.
TANAGA I.
NORTH PACIFIC OCEAN
MID-MAY
LATE MAY

Fig. 4 - Fishing area during May.

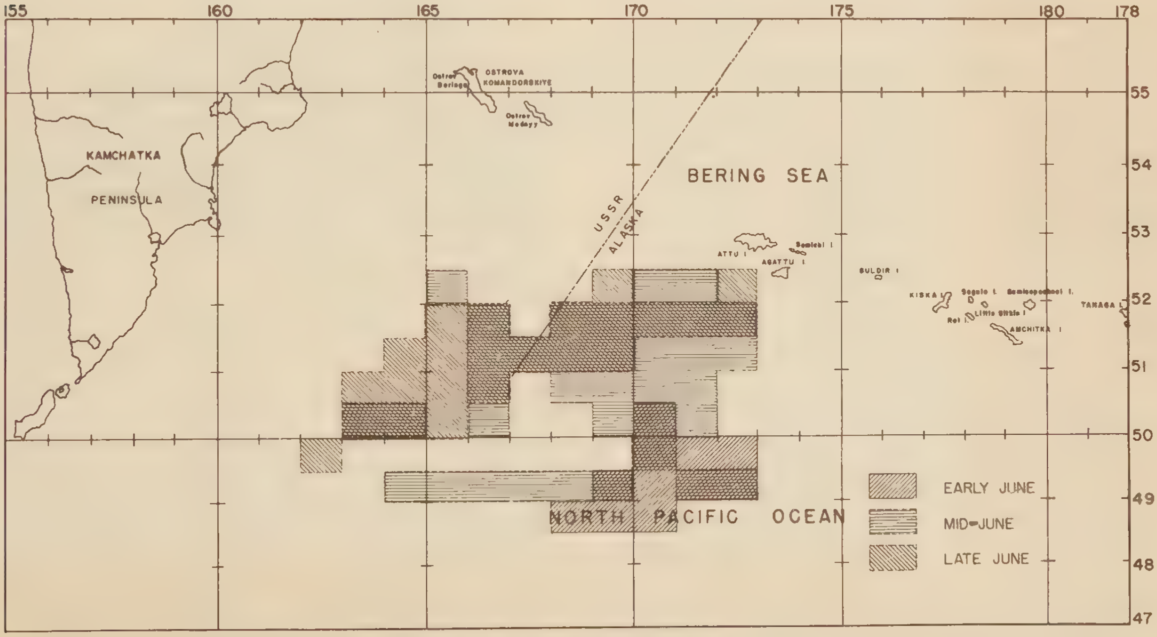
Table 5 - Monthly Performance of the *Miyajima Maru* Fleet, 1954

Item	May	June	July	August	Total
Total days at fishing grounds . . .	17	30	31	17	95
Actual fishing days	13	28	29	17	87
Rest days	4	2	2	0	8
Boat days fished	433	923	947	558	2,861
Total tans fished	58,876	194,332	225,888	137,015	616,111
Average number of tans fished per day per catcher boat	136	211	239	246	215

Communication was an important factor in the deployment of the fleet and in determining areas to be fished. A communication schedule was maintained between catchers and motherships twice daily, from 1600 to 2000 hours (after the gear was set), and again at about 0400 hours (while the set was being, or had been, retrieved). In the evening, catchers reported position, direction of set, number of units set, surface water temperature, water color, water transparency, and related meteorological data. In the morning schedule, the catchers reported progress in gear hauling, catch by species to that time, and the direction in which the fish were moving as ascertained from the face of the net in which the fish were "gilled." These data were inspected and analyzed by the fishing experts and collated with data from other sources. The fishing area for the day was determined as soon as the data were analyzed, this being very soon after morning reports of catchers were received. The following factors were considered in determining fishing grounds:

1. Experience gained from previous years of fishing with respect to the path of migration of salmon through the authorized fishing area.
2. Reports of the exploratory boats which operate a considerable distance away from the motherships.
3. The previous night's catch, e.g. direction of migration of salmon and abundance, size, and species composition of catch and stomach contents of samples from catch.
4. Performance of competing fleets and their positions; this is not only an ethical consideration, but also desirable because moving to areas occupied by other fleets leads to confusion and congestion of gear due to numbers and proximity of catchers.
5. Weather and sea conditions (regardless of the presence of fish, fleets cannot operate practicably when weather is very bad).
6. Position of mothership limited to authorized area.
7. Intuition is also considered to be a factor in deciding upon a fishing area.

FISHING GEAR: As in previous years, gill nets were used exclusively in this operation. A detailed diagram of a "tan" (one unit of gill net) is shown in fig. 2. All dimensions were converted from Japanese units to English equivalents where possible. For specifications of the cordage, a sample of the gear was examined by an experienced netmaker who provided descriptions for comparable American cord-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AMCHITKA I
TANAGA I.
NORTH PACIFIC OCEAN
EARLY JUNE
MID-JUNE
LATE JUNE

Fig. 5 - Fishing area during June.

age. The webbing is of a synthetic material bearing the trade name "Amilon." "Amilon" is very similar to nylon but reportedly has less stretch factor and good knot-holding qualities. The nets were fished in strings of from 200 to 300 "tans" (one unit of gill net), with each catcher and exploratory boat fishing such a string. The extensions of float and lead lines of adjoining units were linked and knotted. Webbing on the units were fastened by a cotton or nylon drop line, interlaced on the breast lines of adjoining units.

Table 6 - Cumulative Salmon Catch of All Seven Fleets by Species--Biweekly Totals

Date	Red	Chum	Pink	Silver	King	Total
	. . . . (Number of Fish)					
May 31 . . .	462,365	940,050	4,916	15	750	1,408,096
June 15 . . .	905,071	2,334,259	63,328	18	2,464	3,305,140
June 30 . . .	1,487,253	4,723,079	216,440	147	8,535	6,435,454
July 15 . . .	2,249,789	6,119,194	1,256,515	67,563	17,723	9,710,784
July 31 . . .	3,405,162	8,546,171	3,974,389	459,222	40,834	16,425,778
Aug. 15 . . .	3,710,434	9,229,298	5,709,108	1,265,896	63,478	19,978,214
Aug. 24 . . .	3,817,159	9,375,620	5,802,196	1,398,066	75,107	20,468,148

The color of most of the webbing used was raw sienna to burnt umber; however some catchers and exploratory boats used various colored webbing experimentally. In the opinion of the fishing experts, dark-gray webbing was better for fishing in the clear waters of the high seas and the color of the webbing of no apparent significance when fishing in the turbid waters nearer the coast of Kamchatka (western fishing area).

METHOD OF FISHING: When the mothership had determined the fishing area for the day, catcher boats were deployed around the mothership within a radius of 50 miles. Within this area catcher boats selected their own fishing areas.

On the high seas one very rarely sees visible signs of salmon or bait abundance, i.e. no "finners," "jumpers," or aggregations of birds. Therefore the fishermen depend almost entirely upon hydrographic conditions to locate areas for setting gear. From past experience Japanese fishermen have found that areas of confluence of currents are abundant in salmon fishing. Temperatures are taken at frequent intervals while under way to find areas where abrupt changes in temperature occur. Records of water color are kept, and prior to setting gear a Secchi disc is lowered to determine limits of visibility (or water transparency). The method of setting gear was similar to that described for the Japanese high-seas salmon fishery of 1952 (Fukuhara 1953). The gill nets were paid out over stern rollers while the catcher was under way. About $1\frac{1}{2}$ to 2 hours were required to set 250 to 300 "tans." In the past, gill-net sets were made either into the wind or with the wind. However, this year fishermen reportedly set gill nets with respect to direction of movement of the salmon, regardless of wind direction (except in very strong wind). Salmon in the area

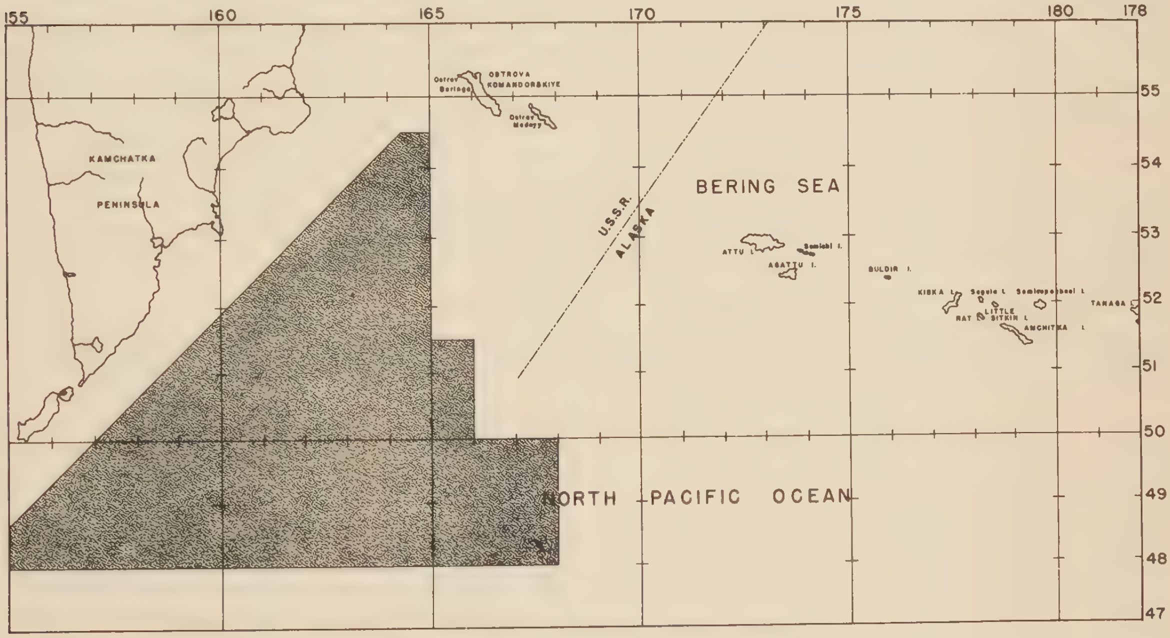
Table 7 - Salmon Catch of All Seven Fleets by Biweekly Periods

Date	Red	Chum	Pink	Silver	King	Totals
	. . . . (Number of Fish)					
May 16-31	462,365	940,050	4,916	15	750	1,408,096
June 1-15	442,706	1,394,209	58,412	3	1,714	1,897,044
June 15-30	582,182	2,388,820	153,112	129	6,071	3,130,314
July 1-15	762,536	1,396,115	1,040,075	68,416	9,188	3,275,330
July 16-31	1,155,373	2,426,977	2,717,874	391,659	23,111	6,714,994
Aug. 1-15	305,272	683,127	1,734,719	806,674	22,644	3,552,436
Aug. 16-24	106,725	146,322	93,088	132,170	11,629	489,934
Total	3,817,159	9,375,620	5,802,196	1,398,066	75,107	20,468,148

were thought to be migrating in an easterly or westerly direction, the latter predominating. Therefore gill nets were generally set in a northerly or southerly direction.

Experience of the Japanese in 1952 and 1953 indicated that in the clearer waters of the high-seas areas gear competition resulted unless the interval between gill nets was at least five miles. Therefore on extremely foggy days the mothership took bearings of all ships in the fleet and partially supervised the deployment of the catchers.

Figure 3 shows a sketch of a drift gill net in operation. All gear of the Nippon Suisan fleet was fished completely detached from the catcher boats. While the gear was "soaking," catcher boats maneuvered to keep the lights in sight. Light No. 1 was generally red. In addition to maintaining a position within sight of the light, the catcher boat remained clear of the gill net by keeping the white lights (lights #2 and #3) behind the red light. The number of "tans" between lights was changed with conditions of visibility. The radio buoy shown in the figure was used only by the exploratory boats. This was felt to be an excellent device for locating gear, however, its use on the gear of all catcher boats was thought to be impractical unless each catcher was assigned its own operating frequency.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RAT I.
AMCHITKA I.
TANAGA
NORTH PACIFIC OCEAN

Fig. 6 - Fishing area during July and August.

Usually gear was started aboard between midnight and 0100 hours. With the exception of exploratory boats, all catcher boat crews retrieved gear by hand. Gear was hauled in by hand at the rate of 41 to 45 "tans" per hour. Thus gear retrieving required from five to seven hours (for a string of 200 to 300 "tans") depending upon the weather and the size of the catch. Exploratory boats used net haulers experimentally. The net hauler was in fact a line hauler, which pulled only on the lead line, while the slack in the float line was pulled in by hand. The method of handling gear while retrieving was described in the report on the 1952 Japanese salmon fishery (Fukuhara 1953).

HYDROGRAPHIC CONDITIONS: Surface water temperatures in the area in which the seven fleets operated during the 1954 fishing season ranged from 2.8° C.

(37° F.) in May to 11.8° C. (53.2° F.) in August. Water color for the same period was from 3 to 7 on the Forel scale, generally increasing with westward movement and advance in season. This corresponds in color to a range from bluish-green to yellow-green. Limit of Secchi-disc visibility increased from about 13 meters in mid-May to about 15 meters in early June, decreasing again to about 7 meters in August. The average surface water temperature, water color, and limit of Secchi-disc visibility, calculated from the daily log entries of the 33 catchers of the Miyajima Maru fleet, from May 14 to August 5, are listed in table 4.

A summary of the Miyajima Maru fleet's fishing schedule is given in table 5.

THE CATCH

During the 1954 season the combined fleets took a total of 20,468,148 salmon, of which 3,817,159 were red salmon (Oncorhynchus nerka), 9,375,620 chum salmon (O. keta), 5,802,196 pink salmon (O. gorbuscha), 1,398,066 silver salmon (O. kisutch), and 75,107 king salmon (O. tshawytscha). Table 6 shows the cumulative catch by species for biweekly intervals. The catch for biweekly periods is given in table 7. The general areas in which these fish were taken are plotted by month; figure 4 shows the fishing area for May, figure 5 shows the fishing area for June, and figure 6 the fishing area in July and August. In addition to salmon, steelhead trout (Salmo gairdnerii) and Dolly varden trout (Salvelinus malma) were landed occasionally.

Table 8 - Catch Per Unit of Effort--Miyajima Maru Fleet

Species	Number of Fish Per Tan For:				
	May	June	July	August	Entire Period
Red	1.47	1.13	2.23	0.69	1.47
Chum . . .	3.16	3.48	2.88	1.36	2.76
Pink	0.02	0.26	1.69	1.64	1.06
Silver . . .	0	0	0.32	0.95	0.33
King	0	0.01	0.03	0.05	0.03
Total . .	4.65	4.98	7.09	4.69	5.65

Table 9 - Average Weight[1] of Individual Salmon by Species and Date

Month	May				June				July				August			
Species	Red	Chum	Pink	Silver	Red	Chum	Pink	Silver	Red	Chum	Pink	Silver	Red	Chum	Pink	Silver
Day	. . . .(In Pounds).															
1					4.5	4.4	2.8		4.7	4.2	2.8	4.8	4.7	4.2	3.0	5.5
2					4.0	4.1	3.0		4.7	4.3	2.9	4.8	4.7	4.7	3.0	5.5
3									4.5	4.3	3.0	4.6	4.6	4.2	3.0	4.6
4									4.6	4.4	3.2	4.8	4.2	4.1	3.0	5.3
5					5.0	4.3	2.8		4.8	4.3	2.8	5.1	4.3	4.1	3.0	5.5
6					4.9	4.3	3.0		4.5	4.2	2.7	4.9	4.0	4.2	3.1	5.2
7					4.0	4.3	2.9		4.5	4.3	2.8	4.3	4.6	4.1	3.2	5.2
8					4.1	4.1	2.8		4.3	4.4	2.9	4.9	4.1	4.0	3.0	5.2
9					4.0	4.1	2.9		4.6	4.3	2.8	4.6	4.1	4.2	3.0	5.7
10					4.1	4.1	2.7		4.1	4.3	2.9	4.7	4.0	4.5	3.0	5.4
11					4.0	4.1	2.8		3.7	4.2	3.0	4.8	3.6	3.9	3.0	5.7
12					4.0	4.2	3.0		4.2	4.6	3.1	4.8	3.5	4.1	3.1	5.5
13					4.7	4.1	3.0		4.3	4.3	3.0	4.9	3.5	4.8	3.2	5.4
14					5.1	4.3	3.2		4.1	4.3	3.0	4.9	3.4	4.2	3.2	5.6
15	4.6	4.9	2.3		4.5	4.3	2.5		4.2	4.4	3.1	4.9	3.5	4.0	3.1	5.6
16	5.0	4.8	2.5		4.5	3.6	2.9		5.3	4.4	2.9	5.1	3.6	4.0	3.2	5.6
17	5.0	4.8			5.0	4.4	3.2		4.5	4.4	3.3	5.0	3.4	4.1	3.1	5.7
18	5.0	4.9			4.9	4.3	3.1		5.1	4.7	3.1	4.9				
19	5.0	4.6	2.6		5.2	4.6	3.1		5.0	4.8	3.2	5.0				
20	5.2	4.7	2.5		5.2	4.4	2.6		4.8	5.0	3.0	4.7				
21	5.2	4.4	2.6		5.3	4.4	3.0		4.8	4.2	3.2	4.9				
22	4.8	4.7	2.5		5.6	4.5	3.1		4.7	4.1	3.0	4.7				
23	4.5	4.5	2.3		5.5	4.7	3.0		4.5	3.9	3.1	4.7				
24	4.5	4.2	2.3		5.1	4.3	3.0		4.5	4.2	3.1	4.7				
25					5.1	4.3	3.1		4.0	4.0	3.0	4.9				
26	4.7	4.3	2.7		5.0	4.7	3.2		4.2	4.2	3.0	5.0				
27					4.8	4.7	2.9		4.2	4.3	2.9	4.9				
28					4.8	4.5	2.8		4.7	4.6	3.2	5.0				
29		4.4	2.6		5.0	4.2	3.0		5.0	4.4	3.0	5.2				
30	5.0	4.4	2.9		5.1	4.4	3.0		5.0	4.7	3.0	5.0				
31	5.0	4.4	2.6						5.0	4.3	3.1	5.3				

[1] From samples of 100 fish.

A monthly summary of the catch per "tan" (one unit of gill net) of the Miyajima Maru fleet is shown in table 8. These figures must be considered only as rough indices of abundance due to variations in mesh size (which were not reported by catcher boats) and peculiarities in the reporting of effort statistics.

Personnel of the Nippon Suisan Co., Ltd. took average weights of salmon in the landings throughout the entire fishing period. These data are given in table 9. The average weights are based on samples of 100 fish of each species per day, specimens being selected at randon from the fish bins. Sampling was generally done at the close of the day's deck activities or after the last catcher boat of the day was unloaded.

CONCLUSION

The areas utilized by the 1954 Japanese high-seas salmon fleet were generally the same as those fished in 1952 and 1953. A comparison of certain pertinent features of the 1952, 1953, and 1954 high-seas salmon fisheries appears in table 10. In 1952 and 1953, three motherships participated in the fishery, and the entire catch was either frozen or salted. Four additional fleets entered the fishing in 1954, three of these equipped with canning facilities.

Table 10 - Comparison of Fishing Seasons, Facilities, and Performance of the Three Post-World War II Japanese High-Seas Salmon Expeditions

Item	1952	1953	1954
Fishing season (inclusive dates)	May 10-Aug. 10	May 10-Aug. 12	May 15-Aug. 23
Number of motherships	3	3	7
Processing facilities of motherships	Freezer & saltery	Freezer & saltery	Freezer, saltery, and two ships each with 2-line cannery, 1 ship with 1-line cannery.
Number of catcher boats[1/]	60	105	194
	(Number of Fish)		
Catch by Species:			
Red	737,489	1,553,107	3,817,159
Chum	638,571	2,707,363	9,375,620
Pink	701,157	3,064,439	5,802,196
Silver	1,365	430,611	1,398,066
King	24,205	8,053	75,107
Total	2,102,787	7,763,573	20,468,148
Catch target	1,800,000	5,487,000	14,072,440
Number over target	302,787	2,276,573	6,395,708

[1/] Approximate number.

The number of catcher boats was increased from about 60 in 1952 to about 105 in 1953. In both these years, gear with "rami" (China grass) webbing was used, with each catcher setting about 100 to 150 units of gear. With the increase in catcher boats, the 1953 fleet took 7,763,573 salmon, an increase of 5,660,786 fish from the initial year's (1952) operation. In 1954 the number of catcher boats was increased by about 90 over the previous year and 134 over 1952.

The number of units set per day per catcher boat in 1954 was almost twice that of the preceding two years. Webbing was changed from "rami" to "Amilon," the latter reportedly more efficient in catching fish. This increase in effort and change in webbing resulted in a total catch in 1954 of 20,468,148 salmon; which exceeded total salmon landings of 1952 and 1953 by 18,365,361 and 12,704,575, respectively. Sevveral factors may have contributed to the progressive increase in salmon landings in the three successive years:

1. Increase may reflect to some degree an increase in abundance of salmon in the areas fished by the fleets. However, accurate estimates of abundance cannot be made using data at hand.

2. Increased proficiency in fishing methods, improved gear, and further knowledge of the fishing area undoubtedly contributed to better performance by the fleets. Modification and improvement of gear is reportedly a factor.

3. The most obvious factor, however, seems to be the progressive increase in effort in the form of more catcher boats and more gear set by each catcher boat.

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RECENT ADVANCES IN THE STUDIES OF THE STRUCTURE AND FORMATION OF THE SHELL OF CRASSOSTREA VIRGINICA

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Knowledge of the structure and formation of an oyster shell has not advanced far enough to enable us to give a complete story of this complex and extremely interesting problem. Like many other marine invertebrates, oysters extract calcium salts from sea water and deposit it in their shells. In this way millions of tons of calcium salts are taken annually from sea water and deposited in the living bodies of the animals. After their death they accumulate on the bottom. The calcareous material is partially redissolved, though the process is slow, depending on local conditions, chemical composition of shell material, and the amount of carbon dioxide in sea water. Oysters play an important role in the calcium cycle since their shells constitute about 90 percent of their total weight.

Deposition and accumulation of calcareous sediments are the problems of great interest to oceanographers and geologists. The marine biologist, however, is concerned primarily with the biochemical reactions and morphogenetical processes which control the formation of shells. In recent years this problem has attracted the attention of a number of investigators who materially contributed to the understanding of the physiology of calcification and shell formation in mollusks.

Microscopic studies of the sections of an oyster shell show the presence of three distinct elements: (a) a very thin and poorly developed horny layer called periostracum. Its presence in the oyster can be detected on a cross section of the mantle edge, or by examining the edge of the mantle of a living mollusk; (b) a prismatic layer consisting of a series of calcite crystals arranged in a honeycomb pattern (Fig. 1). In Crassostrea virginica this layer is well developed only in the right valve; and (c) a calcite-ostracum layer which comprises the greatest part of the shell material. It has a foliated structure made of flat sheets of calcite arranged either horizontally or at an angle to the surface of the shell.

In many specimens of Crassostrea virginica, C. gigas, and Ostrea edulis, the structure of the shell is complicated by the presence of irregular masses of soft and porous material (known as chalky deposits) embedded between the layers of hard material. They consist of loosely packed minute crystals of calcite. In exceptional cases, the chalky material covers the entire inner surface of the shell but it may be completely absent. About 50 percent of New England oysters in my collection were free of chalky deposits. In the other half the deposits occupied only a part of the shell surface.

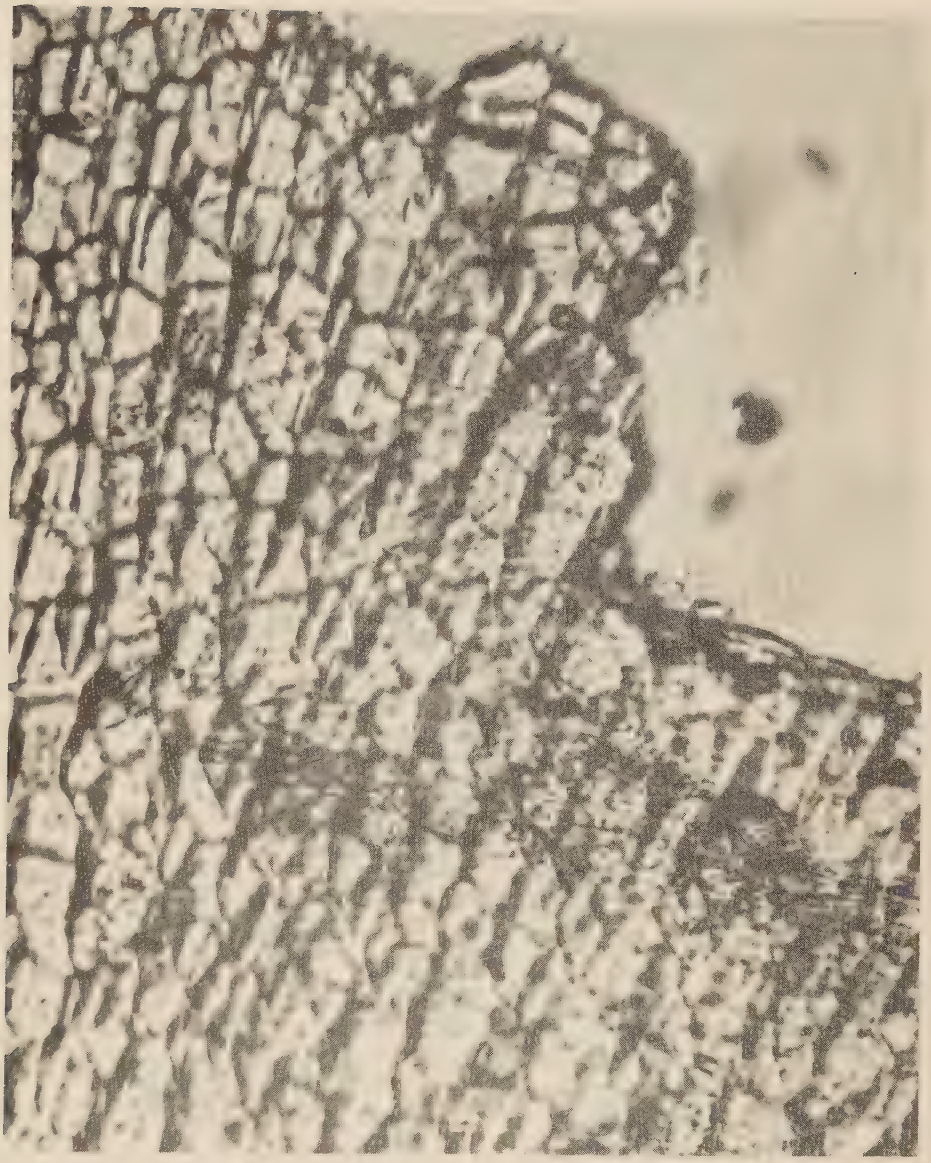

Fig. 1. Prismatic layer at the edge of a growing shell of Crassostrea virginica. Whole mount x 250. Woods Hole, Mass.

Calcium salts of shell can be easily dissolved in dilute mineral acids or in chelating agents such as sodium versenate. The insoluble residue appears in the form of thin, homogenous sheets of organic material kept together like pages of a book. This substance, discovered in 1855 by Fremy, is known as conchiolin. It is a scleroprotein, the structural formula of which has not yet been determined. The elementary composition of conchiolin of Ostrea edulis, according to Schlossberger (1856), is as follows: H, 6.5%; C, 50.7%; N, 16.7%. Wetzel (1900) found that conchiolin contains 0.75 percent of sulfur and Halliburton (quoted from Schmidt, 1928) gives the following formula: $C_{30}, H_{48}, N_9, O_{11}$.

The calcareous material of mollusk shells is laid either as aragonite or calcite. The shells of edible oysters consist exclusively of calcite; on the other hand, the nacreous layer of the pearl oyster consists of aragonite. Taking advantage of the fact that both calcite and aragonite are present in the two distinct layers of shell of the fan oyster (Pinna) and of the pearl oyster (Pinctada), the French investigators (Roche, Ranson, Eysseric-Lafon, 1951) attempted to find whether there is a difference in the organic material of the two layers of the same species. They found a distinct difference in the percentage of the two amino acids obtained from the conchiolin of the prismatic layer (calcite) and of the nacreous part (aragonite) of these mollusks. In the first one the content of tyrosine (11.6-17.0%) and of glycocolle (25-36%) was much higher than in the latter (tyrosine 2.8-6.0%; glycocolle 14.9-20.8%). Conchiolin from the shells of Ostrea edulis was found to contain 3.2 percent tyrosine and 15.7 percent glycocolle. The content of other amino acids found in the shell of O. edulis, namely, arginine, lysine, leucine, valine and methionine varied between 0.45 and 3.55 percent. These findings are interesting, but at present provide no clue concerning the role of various amino acids in determining the minerological type of shell structure.

To the naked eye and under the ordinary microscope the conchiolin appears as amorphous, viscous, and transparent material, which hardens shortly after being deposited. By using electron microscope technique, Florkin of Liege University and his associates (Gregoire, Duchateau, and Florkin, 1950) have shown that the conchiolin of gastropods and lamellibranchs consist of a material laid as a fine network with many meshes of irregular shape and variable dimensions. This can be clearly seen in the photograph of conchiolin of abalone (Haliotis tuberculata) at magnification of 100,000 times. (Fig. 2). It is obvious that the organic membranes of molluscan shells have rather complex structures which can be seen only with very high magnification. It is too early yet to speculate regarding the significance of this structure and its role in calcification.

The question of the amount of conchiolin in the oyster shell was studied by several investigators. As early as 1817 Brandes and

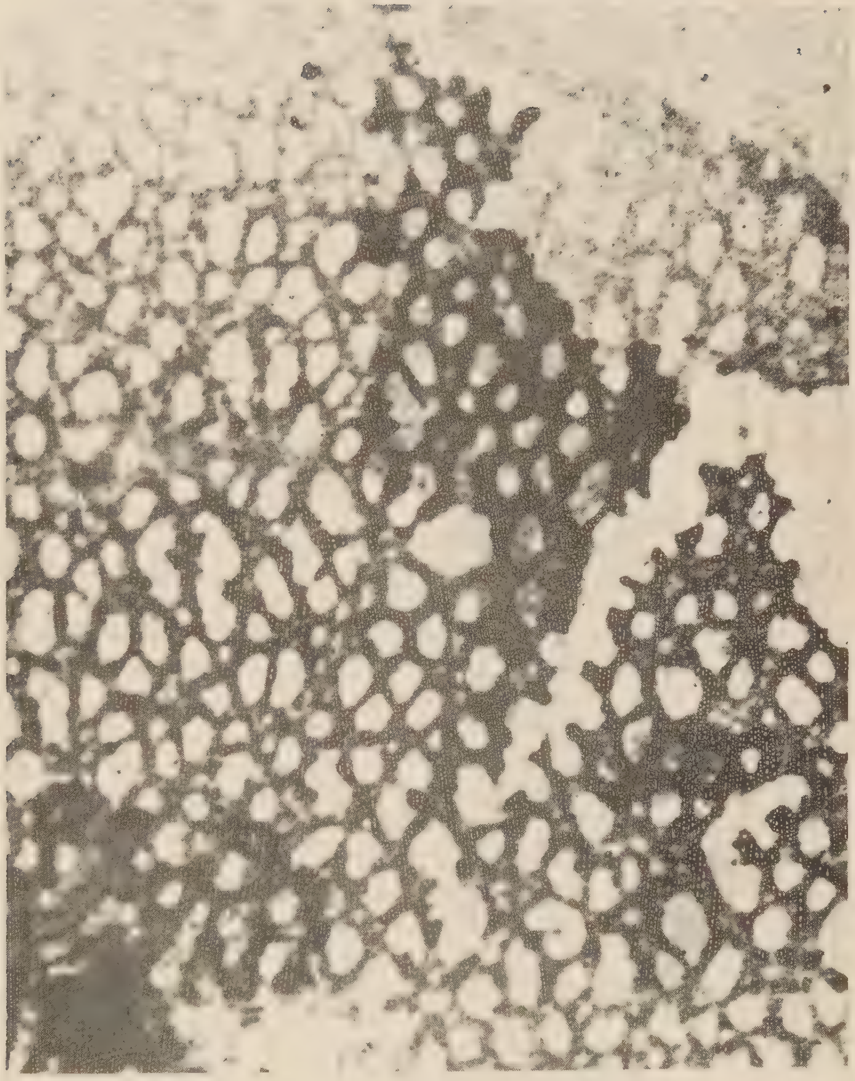

Fig. 2. Conchiolin sheet of the shell of abalone (Haliotis tuberculata) photographed after decalcification and ultra-sonic treatment. Electron microscope; phosphotungtic acid x 100,000. Courtesy of Dr. Ch. Gregoire, University of Liege, Belgium 1.

Bucholz estimated that the entire oyster shell consists of about 98.6 percent $CaCO_3$ and 0.5 percent organic material. Schlossberger (1856) found 6.3 percent of organic matter in the prismatic layer of the oyster shell, but only from 0.8 to 2.2 percent in the calcite ostracum. According to Douville (1936), the albuminoid content of oyster shell is 4.8 percent.

Determinations made for Korringa (1951) by Dr. A. Grijns gave similar results. It is interesting to note that in the latter tests the conchiolin content of the prismatic layer varied from 3.4 to 4.5 percent against the 0.5-0.6 percent in the calcite ostracum. My own observations made this year on Crassostrea virginica from Cape Cod, Narragansett Bay, and Long Island Sound show that in the 34 samples studied, the organic content of the calcite ostracum layer varied from 0.46 to 1.1 percent. There was no significant difference between the organic content of chalky deposits or the hard portions of calcite. Duplicate and triplicate tests of the hard portions of shell of the same specimen show that the conchiolin content is fairly constant, the difference not exceeding 0.2 percent. Among the different specimens, the conchiolin content of the entire shell, varied from 0.3 to 1.1 percent.

The presence of chalky deposits and their structure was subject to many speculations. Orton and Amirthalingam(1927) advanced a theory that chalky deposits occur in places where the mantle epithelium looses contacts with the shell. This theory received support from Ranson (1939-41) who, without making any additional study, stated that chalky deposits are formed wherever there is a local detachment of the mantle from the shell. Korringa finds no difference in the percentage of chalky deposits in the oysters placed with the cupped valves uppermost and in those which are kept in their normal position with cupped valves undermost. He assumes that the topmost mantle epithelium of the exhalant chamber "is certainly liable to sagging". My observations on Crassostrea virginica show that the mantle epithelium adheres rather strongly to the inner sides of the valves and does not sag unless the mantle is pushed down by force.

To determine whether local detachment of the mantle from the inner surface of the shell expedites the formation of shalky deposits, I made the following experiments: Small pieces of thin plastic, about 1 cm.^{2}, were bent in the shape of shallow cups and introduced between the mantle and the shell. In five oysters the concave side of the cup was facing the mantle, in another five the position of the cup was reversed, i.e., its concave side faced the shell. Oysters were kept for 55 days in running sea water in the laboratory. During this time they fed actively and there was considerable shell growth along the margin of the valves. After removal from the shells, the plastic cups were found to be covered with hard calcite deposit. There was not the slightest indication of the formation of chalky material. On the

other hand, conspicous chalky areas were formed along the marginal area of shell growth in places where the two valves were in close contact with each other (Fig. 3). It is clear from these observations that chalky deposits may be constructed by the mantle at any place on the surface of the shell and that the detachment of the mantle epithelium from the inner surface of the valve is not a factor in their formation.

Korringa (1951) advances a theory that "chalky material is used by the oyster as a measure of economy and as a 'cheap padding' in smoothing out the shell's interior and in creating the right shell shape to maintain its efficiency of function. The more the oyster shell attains a cupped shape, the more layers of 'chalky' material are deposited beyond the muscle to maintain the proper shell dimensions." He emphasizes the significance of the presence of chalky deposits beyond the muscle scar and for reasons which he fails to explain disregards their presence in the other areas. The theory goes far beyond the experimental evidence and its teleological approach does not contribute to the understanding of the problem.

Since so much emphasis was placed on the significance of chalky deposits in the area beyond the muscle scar, it was of interest to determine whether there is a definite tendency in the formation of chalky deposits in different parts of the shell. For this purpose the surface of the valve was arbitrarily divided into the four quadrants shown in Figure 4. Examination of several hundred oyster shells of Crassostrea virginica from various parts of the Atlantic Coast showed that chalky deposits were absent in 53.1 per cent of right valves and 47.9 per cent of the left valves. To have some idea of the extent of chalky deposits present, the following categories were established: I. from 1 to 25% of the area of a quadrant covered by chalky deposits; II. from 26 to 50%; III. from 51 to 75%; and IV. from 76 to 100%.

The results, given in Table I, show that the majority of oysters in which chalky deposits of any size were found had less than 25 per cent of the total shell area covered with them.

Table I. Occurrence and Extent of Areas of Chalky Deposits in Crassostrea virginica (percentages); Exclusive of Oysters without Chalky Deposits

Percent of shell surface occupied by chalky deposits	0%	1—25%	26—50%	51—75%	76—100%
Left valve	47.9	25.9	13.6	9.8	2.8
Right valve	53.1	24.9	12.0	8.4	1.5

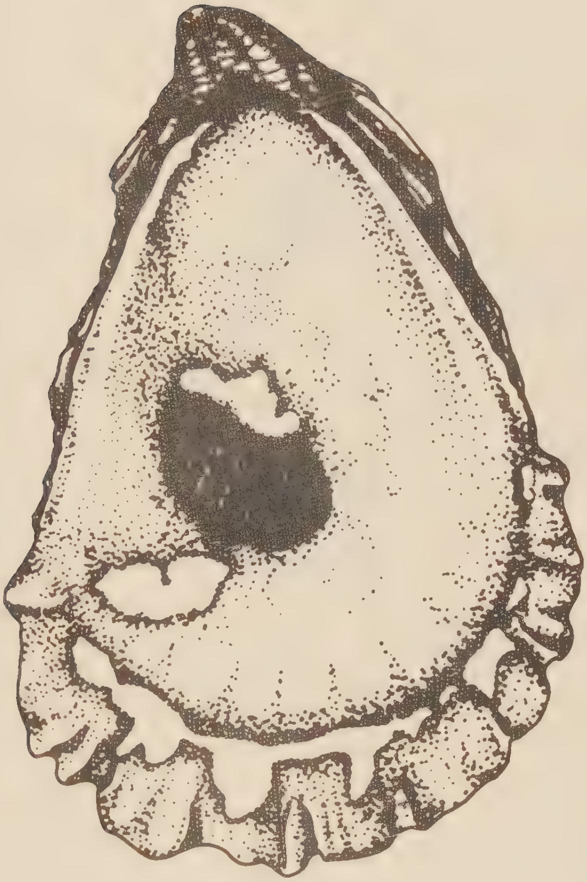

Fig. 3. Chalky deposits (white areas) at the edge of a rapidly growing shell of Crassostrea virginica and near the muscle scar. Woods Hole.

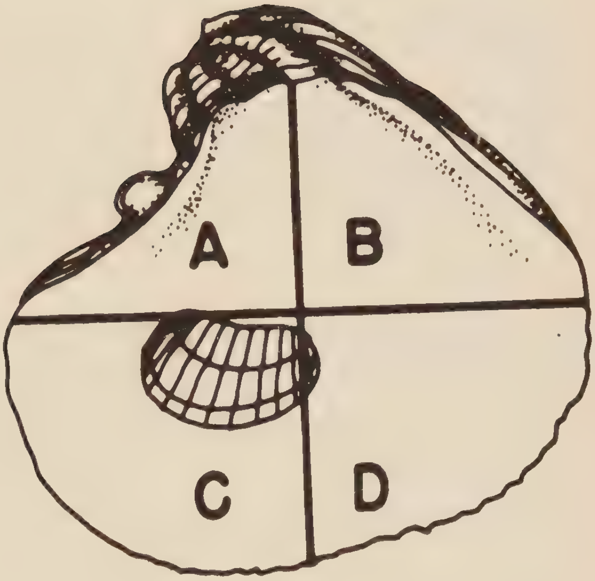

Fig. 4. Four quadrants of the shell area used in a study of the occurrence of chalky deposit in the values of adult Crassostrea virginica.

Chalky deposits of any size were almost uniformly distributed, 48 per cent occurring on the dorsal half (above the muscle scar) and 52 per cent on the ventral half of the shell. The percentage of occurrence among the four quadrants (A, B, C, D) was also rather uniform as can be seen from Table II.

Table II. Occurrence of Chalky Deposits in the Four Quadrants of the Shell (percentages)

Areas	A	B	C	D
Left valve	22.2	25.5	29.8	22.5
Right valve	25.2	23.0	22.9	28.8

Although there seems to be an equal chance for a chalky deposit of small or medium size to be found in any of the four quadrants of the shell, large deposits covering more than three quarters of the area of a quadrant are more frequently found in the dorsal half of the valves (quadrants A and B, Table III.)

Table III. Frequency of Occurrence of Large Areas of Chalky Deposits (Category IV) within the Four Quadrants of the Valves (percentages)

	Areas of the valves			
	A	B	C	D
Percentage occurrence (both valves)	33.3	47.3	10.8	8.6

Studies of the distribution of chalky deposits in Crassostrea virginica do not support Korringa's suggestion that they are purposely formed by the oyster in order to maintain a constant distance between the shells in the posterior area opposite the exhalant chamber.

It is well known that the valves of oysters differ in size and shape, the left valve usually being cupped and heavier than the flat and lighter right valve. Normally the oyster occupies a position with the right (flat) valve uppermost.

The majority of Atlantic oysters, when placed on their left valves with the dorsal end away from the observer, show a curvature to the left. This indicates more rapid growth of the shell along the dorso-ventral axis, with a slight shift of the direction of growth to the left. In very young oysters which frequently appear to be round

this tendency is less pronounced. Examining my collection of shells, I found some oysters in which the growth along the dorso-ventral axis was almost equal to the growth along the anterio-posterior direction. The width of these specimens was almost equal to their length and sometimes even exceeded it (Fig. 5). The growth of shell in any direction is an expression of a metabolic gradient along the given axis. The latter is not definitely fixed in the oyster but changes in response to environment. As a rule, oysters living on soft bottom or in very crowded condition on natural reefs tend to form long narrow shells while their growth in width is suppressed. There are, however, other, apparently intrinsic, factors which cause the change in the direction of growth probably not associated with environmental conditions. In several specimens collected in various parts of the coast the direction of growth shifted from left to right. This can be clearly seen in Figure 6 showing the two left shells of the oysters, one normal and the other with a distinct shift to the right. The "right handed" oysters were found in Texas, Chesapeake Bay, Narragansett Bay, and New Hampshire. There was no indication of the presence of any mechanical obstruction that might have interfered with normal growth. In every other respect the "right handed" oysters were normal and had the typically cupped left valves with well developed grooved beaks. The "right handed" specimens are comparable to the so-called inverted shells in which the typically left valve structures appear on the right side and vice versa. Inversion was found in several pelecypods (Lamy, 1930). In case of Crassostrea virginica, the inversion of growth does not affect the morphological structures but is expressed only in the shifting of the axis of growth.

There is a difference in the physiology of the right and left valves of the oysters. The rate of calcification is significantly higher on the left side than on the right one. This can be easily noticed by examining the newly formed shells. The material secreted by the left mantle is thicker and heavier than the material deposited during the same time by the right mantle. For these observations, conducted since last April, I used adult oysters which had no recently deposited shell areas along the edges of the valves. They were placed in laboratory tanks supplied with running sea water. About two months later the pieces of the newly deposited shell on each valve were carefully removed from the shell. After measuring their areas with planimeter, they were dried at 55°C. and weighed. The results are summarized in Table IV.

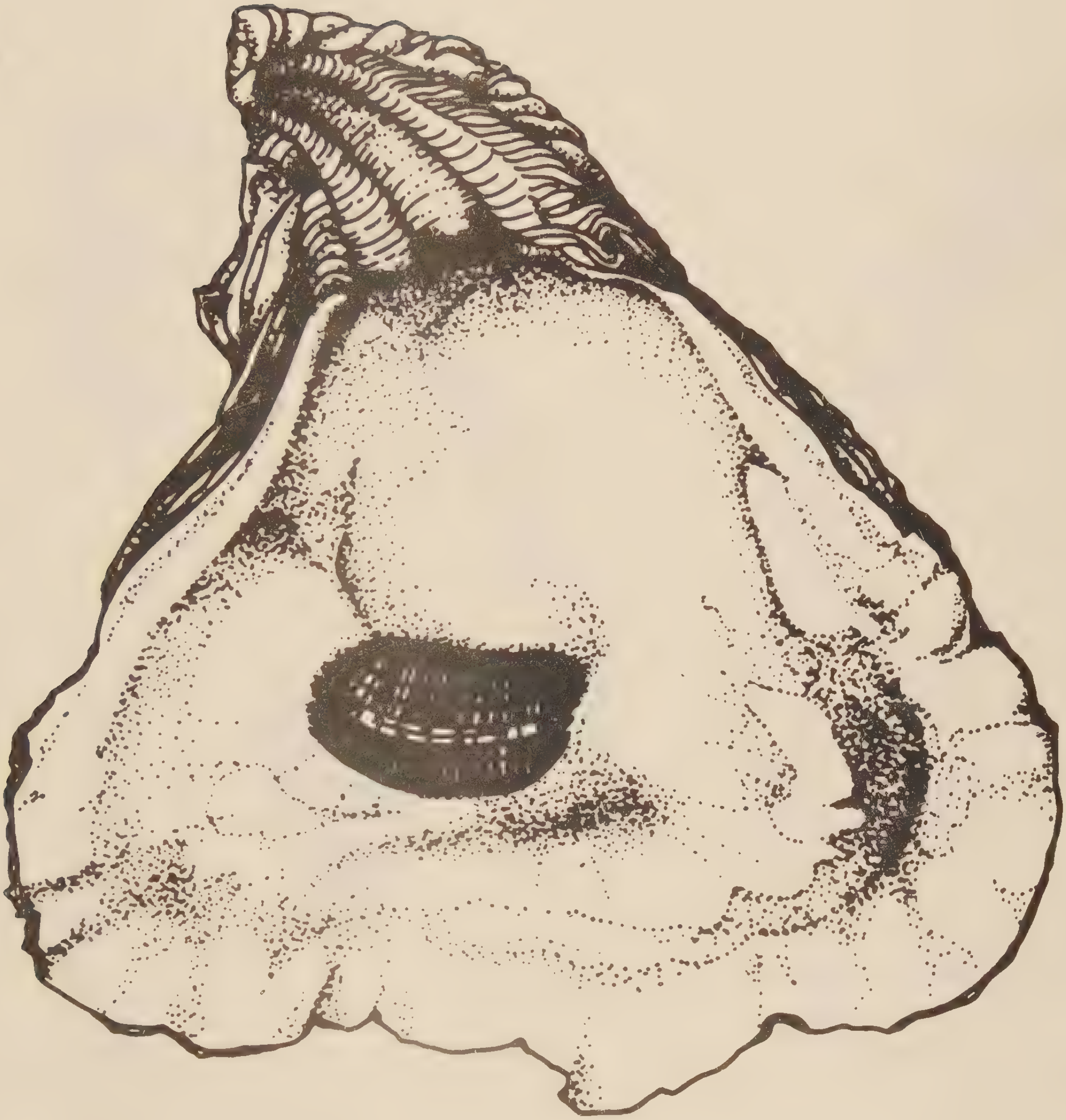

Fig. 5. Large Crassostrea virginica, from Hadley Harbor, Naushon Island near Woods Hole.

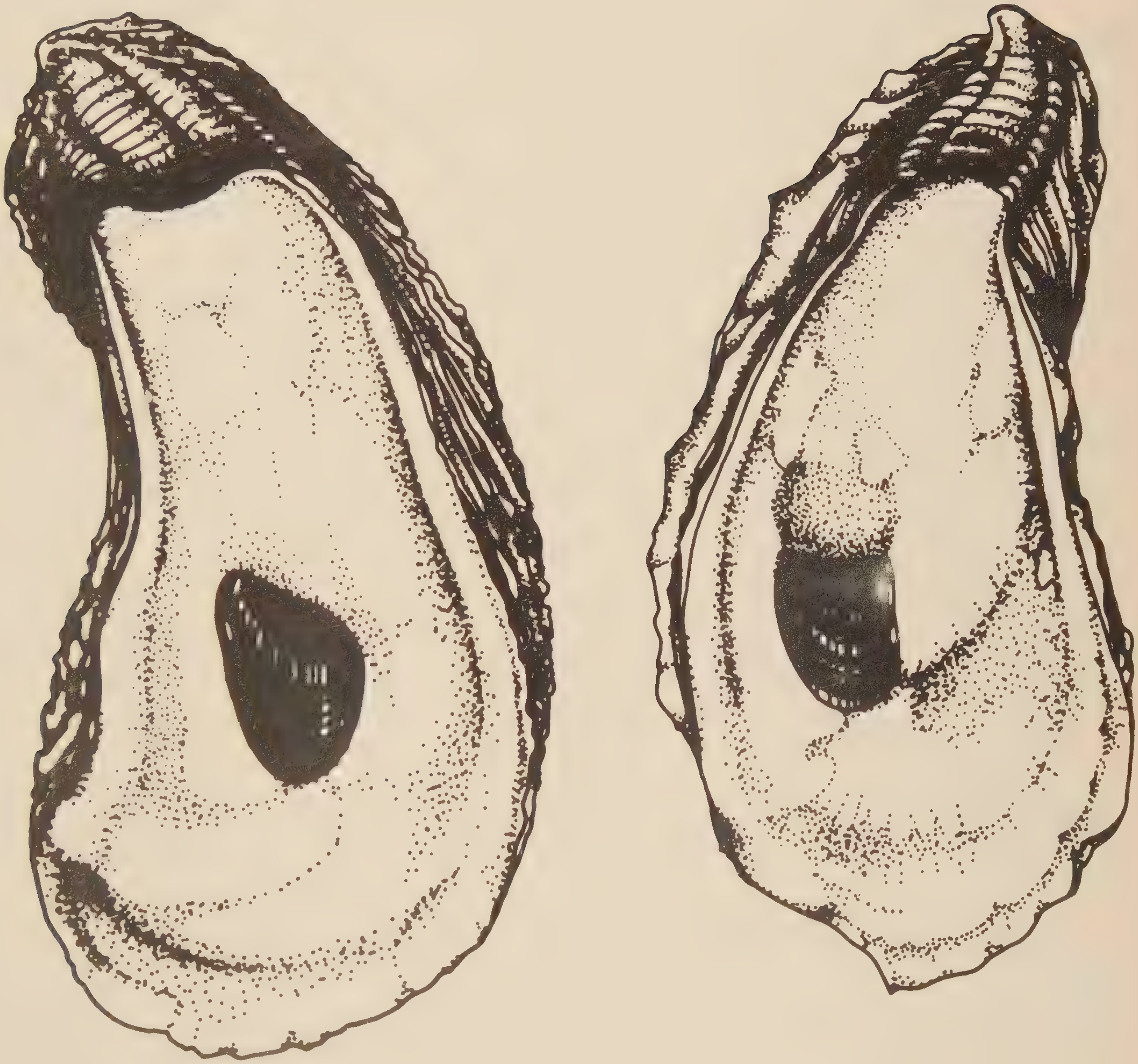

Fig. 6. Two left valves of Crassostrea virginica from Maine (on the left) and from Texas (on the right).

Table IV. Areas of New Growth and Rate of Deposition of Shell Material in Milligrams per Day per Square Centimeter during April -- June, 1954, Woods Hole, Mass.

Oysters	Area of new shell cm^2	Weight per $cm.^2$ (mg.)	Ratio	Ratio L:R. Valve (mg.)	Number of days under observation
Five-year old Narragansett Bay					
Left valve	5.80	156		2.8	55 days
Right valve	5.16	59.3		1.1	
			2.6		
Adult Narragansett Bay					
Left valve	7.1	123		1.8	68 days
Right valve	7.7	19.9		0.3	
			6.2		
Adult Narragansett Bay					
Left valve	6.1	74.2		1.09	68 days
Right valve	8.8	25.5		0.37	
			2.9		
Two-year old New Hampshire					
Left valve	3.68	163.8		2.98	55 days
Right valve	4.20	52.0		0.95	
			3.2		
Old New Hampshire					
Left valve	6.83	71.2		1.3	55 days
Right valve	7.35	33.0		0.6	
			2.2		

In every case the amount of calcified material deposited over a unit of area was considerably greater on the left valve than on the right one, the difference varying from 2.2 to 6.2 times.

The ratio of calcification along the inner portion of the mantle may be studied by inserting small pieces of plastic or other material of known area and weight between the mantle and shell. In interpreting the results one should consider, however, that the presence of a foreign body may produce pathological conditions which upset the normal rate of calcification. The results obtained with this method show great variability. Observations made with 16 adult oysters at Woods Hole during the period of August 9-20, 1953, show that in 15 specimens the daily rate of shell deposition per square centimeter varied from 0.4 to 2.1 milligrams. One oyster deposited 14.2 milligrams in two days or 7.1 mg. per day. Data obtained this spring with the Narragansett Bay oysters kept in laboratory tanks for 68 days during the period of April-June show the variation from 0.1 to 0.79 mg. per day per square centimeter. In one oyster the rate of deposit under a plastic cup was 16.4 mg. per day. In some oysters the presence of plastic material produced pathological conditions which resulted in the formation of leathery capsules similar to the blisters frequently found in the area of the adductor muscle. These experiments are being continued using various techniques designed to minimize the effect of local stimulation of shell secreting tissues.

French physiologist Monnigault (1939) apparently was the first one to point out the role played by phosphatase as a factor in the acceleration of shell formation. This enzyme is probably an agent in the transfer of calcium. Later on, Bevelander and Benjer (1948) apparently unaware of Monnigault's work arrived at the same conclusion. Freeman and Wilber (1948) have demonstrated the presence of another enzyme, carbonic anhydrase, in the mantle tissues and body fluids of some pelecypods and gastropods. While this enzyme may be important in shell formation in some species, its negligible activity in other mollusks suggests, however, that shell may be deposited in its absence.

Physiological and histological studies on growth and regeneration of shell of the oyster disclose the great complexity of the process. The role played by different parts of the mantle epithelium in secreting conchiolin and in depositing calcium carbonate in the form of well arranged prisms of the prismatic layer or as densely packed lamellae of the calcite presents a stimulating problem of research.

Observations made in my laboratory on isolated pieces of mantle and on the mantle edge after the removal of a portion of the shell show that clear, viscous, sometimes stringly conchiolin is secreted from the periostracal groove located between the outer (secretory) and the middle (sensory) folds of the mantle. The sensory fold is capable of great extensibility and seems to serve as a temporary support for the viscous

conchiolin until the latter hardens. This conclusion is confirmed by the examination of the sections of mantle which clearly show that conchiolin produced at the mantle edge originates in the periostracal groove. The results are in agreement with the observations made by other zoologists on the shells of O. edulis and Anodonta.

Mucus secreted by the mantle of the oyster contains a large number of blood cells. Their role in calcification is not yet understood. The newly deposited material contains minute granules which sometimes give a positive reaction for calcium with alizarin and other reagents used for identification of this metal. Unfortunately, none of the available color reactions for the detection of calcium are dependable for they often give negative results. Because of this technical difficulty, it has been impossible to trace the origin of the tiny granules known as calcosphaerites (Fig. 7) which appear in the conchiolin shortly after it is secreted by the mantle. The growth of these crystals and the formation of large crystalline units which eventually form the prismatic layer (Fig. 1) can be seen on the black and white enlargements of Kodachrome photographs made with the polarizing microscope (Figs. 8 and 9). In polarized light these crystals of calcite present a picture of great brilliance and beauty.

The conditions under which the calcium carbonate forms the prisms of the prismatic layer or is deposited as a foliated structure of the calcite ostracum are not known. The problem presents an opportunity for further research of calcification.

In conclusion, I want to remark briefly on the source of calcium used in the formation of the shell of Crassostrea. In 1938, Robertson and Prentice pointed out that sea water is the source of calcium for building the tubes of an annelid worm, Pomotoceros triqueter. I indicated at that time (Galtsoff, 1938) that calcium salts required for the building of the shells of Ostrea (Crassostrea) virginica are probably taken directly from the sea water. Experimental work by Jodrey (1953) using Ca_{45} clearly shows that pieces of oyster mantle separated from other tissues are able to deposit calcium taken directly from sea water. She also shows that the rate of calcium turnover in the edges of the mantle is about twice as rapid as in the interior of the mantle. The use of radioactive isotopes gives a new tool for solving many present mysteries connected with the formation, maintenance, and growth of shells of oysters and other marine invertebrates.

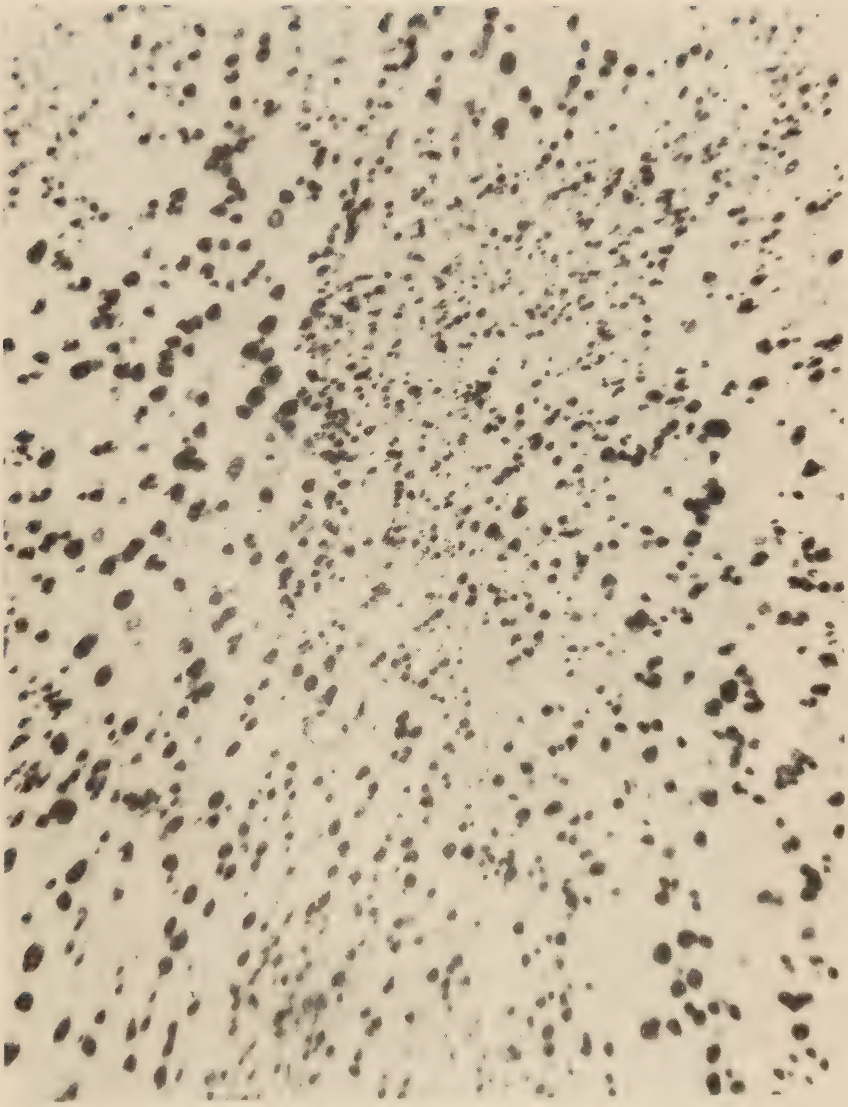

Fig. 7. Small granules (calcospaerites in conchiolin shortly after it had been secreted by the mantle. Black and white enlargement of a Kodachrome photograph taken in polarized light. Highly magnified.

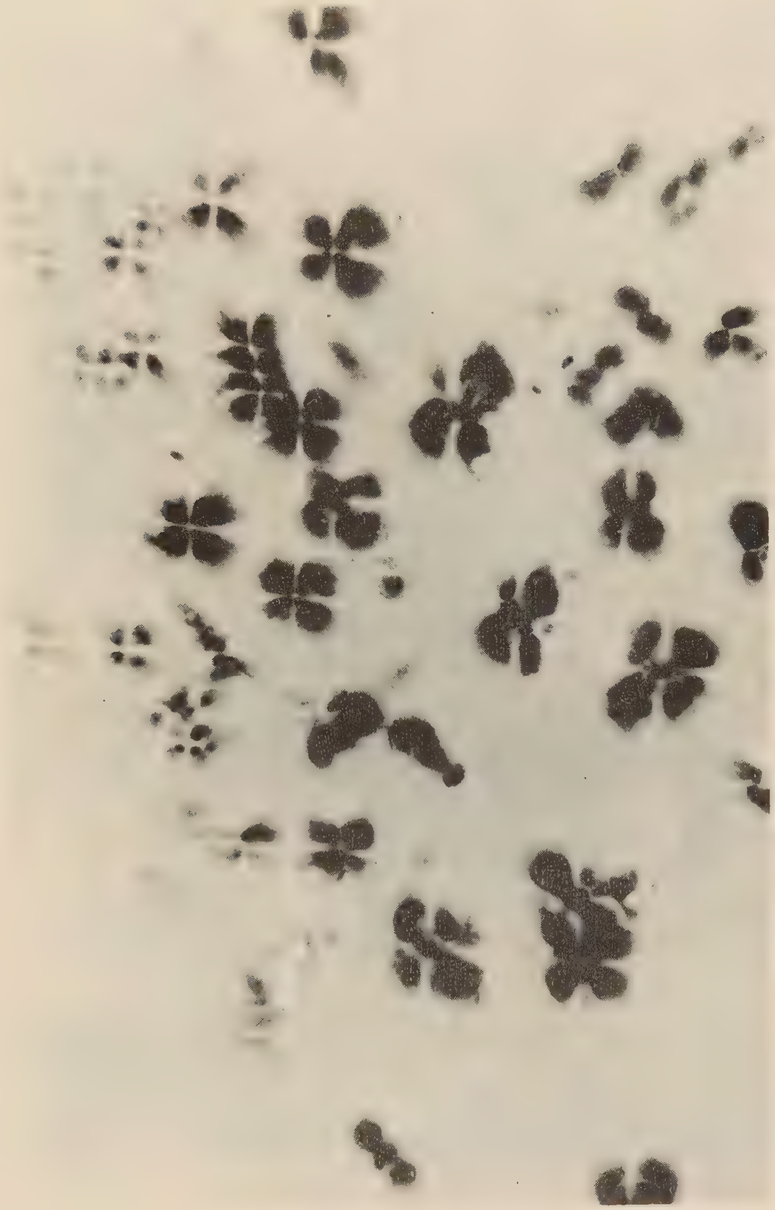

Fig. 8. Calcite crystals found in conchiolin 24-48 hours after it had been secreted. Black and white enlargement of a Kodachrome photograph taken in polarized light with the magnification of X 250.

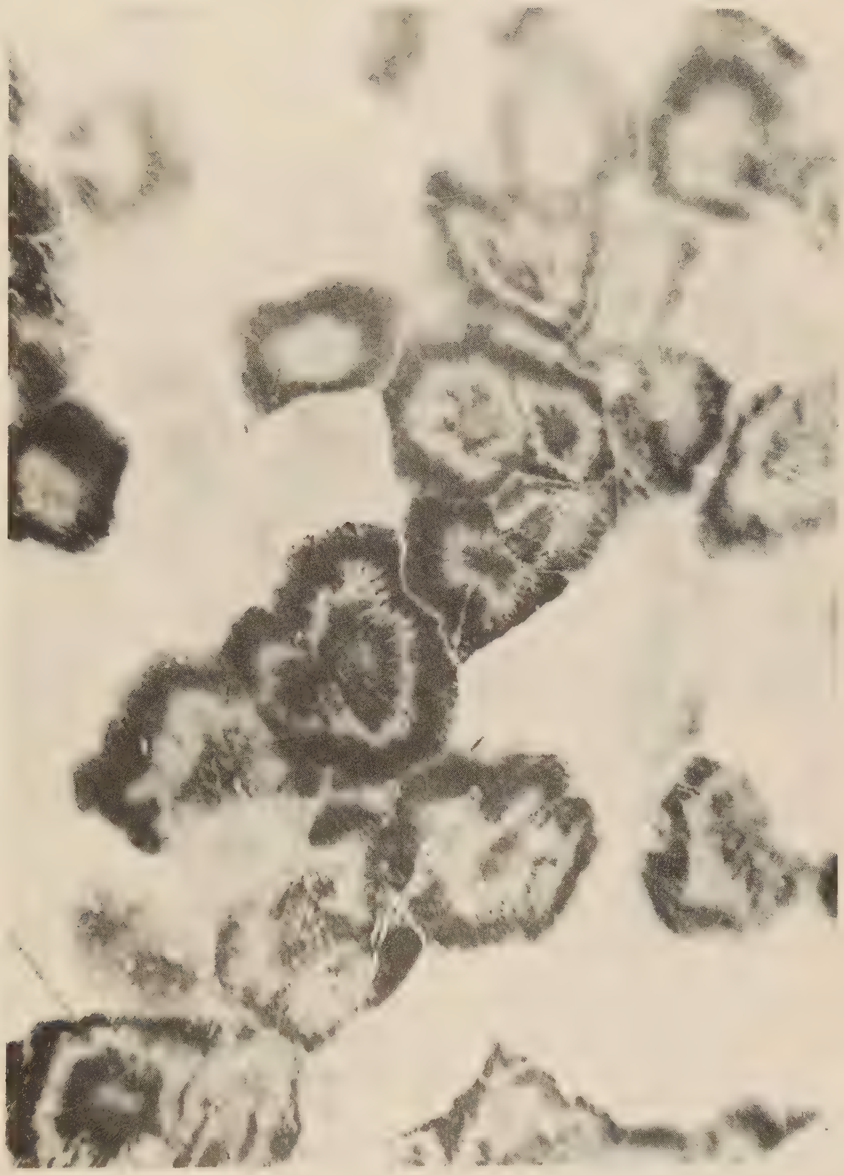

Fig. 9. Large calcite crystals at the beginning of the formation of the prismatic layer. Black and white enlargement of a Kodachrome photograph taken in polarized light with the magnification of X 250.

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EXPERIMENTAL HATCHING OF KING SALMON IN MILL CREEK, A TRIBUTARY OF THE SACRAMENTO RIVER[1]

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INTRODUCTION

In the fall of 1952 survival studies on the eggs of king salmon (*Oncorhynchus tshawytscha*) were conducted on Mill Creek, Tehama County, California, a tributary of the Sacramento River. These were a part of a study investigating freshwater influences on survival rates of salmon near the southernmost limit of their spawning range. The reasons for widely fluctuating survival rates of salmon from year to year are being sought by fishery biologists in an effort to improve management techniques.

Grateful acknowledgement is extended to Robert Azevedo and James Miggens of the Branch of Game-Fish and Hatcheries, and to Don A. LaFaunce and Harry P. Chandler of the California Department of Fish and Game, for their assistance in conducting this experiment.

EXPERIMENTAL PLAN

Carl (1940), in an experiment involving silver salmon eggs buried in gravel in a hatchery trough, found that 8 percent of the eggs were unaccounted for following hatching. Since the design of the present experiment required that an accurate account be kept of a known number of salmon eggs in the gravel, any influence the containers enclosing the samples might have on survival had to be sacrificed.

The experimental plan called for 100 sample plants of 100 eggs each. An additional 10 sets of 100 unfertilized eggs were planted for comparison of their rate of decomposition with that of the test plants, and another five groups of fertilized eggs were planted as controls.

A long riffle adjacent to the old Mill Creek hatchery at Los Molinos, California, was selected for the study (Figure 1). The bottom was of large gravel cemented to the stream bed. Even though natural spawning occurred here each year the rubble found in the riffle did not appear to be entirely satisfactory for natural spawning and was supplemented with five cubic yards of three-fourths inch gravel.

Five rows of 23 nests each were used, making a total of 115 groups of eggs. The nests were spaced in rows one meter (39 inches) apart. Each row of five nests was marked with lengths of pipe driven into the banks. The nesting areas were prepared by removing gravel to form a pocket in the bed, 6 to 10 inches deep and about 18 inches in diameter.

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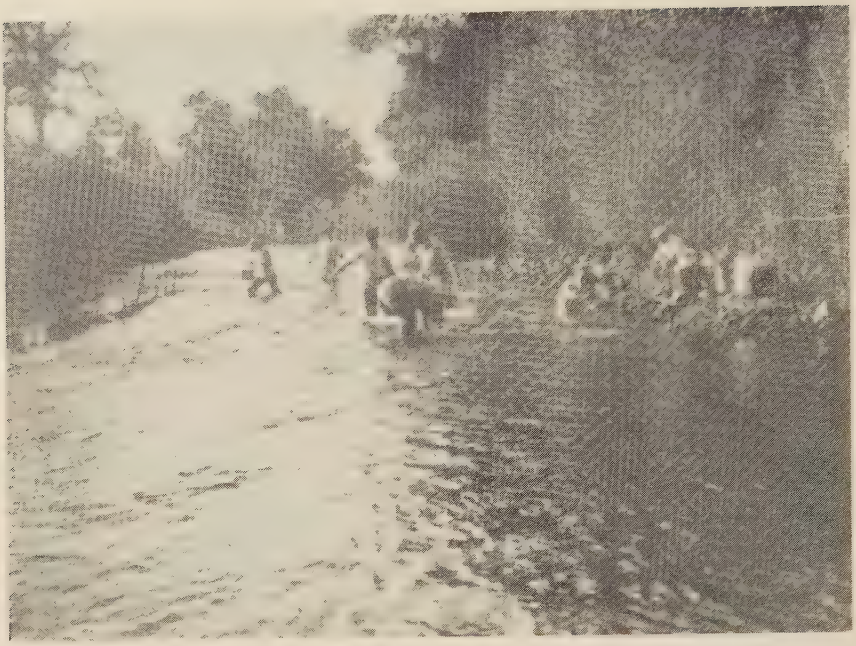


FIGURE 1. Riffle in Mill Creek, Tehama County, selected for egg planting, showing pipes marking rows of nests.

The eggs were placed in containers made of gray "Rust-proof Lumite Screening" of 19 meshes per inch and stitched into $5\frac{1}{2}$- x 10-inch bags with orlon thread. A numbered tag was wired to the inside of each bag for identification and the mouth of each bag tied with a length of cotton cord which had a colored tag at the end. Cotton line was found to be inadequate for tying the bags because of its rapid deterioration. Nylon or similar material would be expected to serve much better.

Water temperatures and stream flows were found to be satisfactory for planting on October 29, 1952. On that day fish culturists of the Coleman Hatchery, using standard hatchery techniques, fertilized eggs from six female king salmon. A hundred eggs and about half a pint of gravel were placed in each plastic sack.

The filled sacks were transported to Mill Creek in five 10-gallon milk cans. The water temperature in Coleman Hatchery was 54 degrees F. Upon arrival at Mill Creek, a 40-mile trip which took approximately one hour, the temperature of the water in the milk cans had increased to 58 degrees F. At 1 p.m. the temperature of Mill Creek was 56 degrees F., and the air temperature was 65 degrees F.

The sacks of eggs were distributed at random among the prepared nesting areas in the stream bed. Each sack, marked by one of five different colored tags for identification, was placed in the previously hollowed-out spot and covered with gravel up to $2\frac{1}{2}$ inches in diameter which, when necessary, was supplemented by the extra supply of three-fourths inch gravel that was available. The nests were covered from 6 to 10 inches deep. On October 29, 1952, 11 of the sacks were dislodged by king salmon building nests in the stream. To avoid further losses of this type, the area was covered with wire netting.

RESULTS

The first group of 20 sacks removed from the stream on October 31st, two days after the initial plant, showed a 47.4 percent survival (Table 1). The high mortality of the first group after being in the gravel only two days was evidently due primarily to premature handling and transportation of the eggs. At least some of this mortality could have been avoided by a longer water hardening period. Many of the eggs apparently died upon coming in contact with the plastic screening of the containers.

TABLE 1

Comparison of Egg Conditions in Each Removal Group, With Average Eggs per Sack and Standard Deviations

Group	Removal date	Number of eggs found	Moldy and/or ruptured	Opaque	Clear un-fertilized	Alive
1 (20 sacks)	10/31/52	1,985	0	10	*	948
Mean per sack		99.2	0	0.5		47.4
Standard deviation						8.4
2 (20 sacks)	11/11/52	1,771	856	16	54	845
Mean per sack		98.4	47.6	0.9	3.0	46.9
Standard deviation						11.1
3 (20 sacks)	11/24/52	1,403	694	16	24	669
Mean per sack		82.5	40.8	0.9	1.4	39.4
Standard deviation						11.7
4 (20 sacks)	12/14/52	817	365	108	65	279
Mean per sack		51.1	22.8	6.8	4.1	17.4
Standard deviation						7.1
5 (6 sacks)	2/26/53	263	256	0	7	0
Mean per sack		43.8	42.7	0.0	1.2	0.0
Standard deviation						0.0

* It was impossible to separate clear unfertilized from dead eggs at this stage.

Each of the remaining four groups of 20 sacks was removed at intervals of 238 heat units. Table 2 gives the number of heat units accumulated during the test.

Information on the number of heat units required to hatch king salmon eggs was obtained from staff members of the School of Fisheries at the University of Washington (Figure 2). The number of heat units is calculated by multiplying the number of days of incubation by the number of degrees Fahrenheit above freezing (32 degrees F.) (Wales, 1941). An expected average temperature of 50 degrees F. was used in estimating the number of heat units required to bring the eggs to each stage of development. The observed average temperature was 47 degrees F.

The second group was removed November 11, 1952. During the period that this group was in the gravel the stream flow remained relatively stable, with the temperature of the water cooling slightly as

TABLE 2

Accumulated Heat Units

Date	Daily number heat units	Subtotal upon removal date	Date	Daily number heat units	Subtotal upon removal date
Oct.			Dec.		
29	22.7		1	13.0	
30	22.9		2	14.0	
	—	—	3	12.8	
31	20.8	45.6	4	12.8	
Nov.			5	13.6	
1	20.8		6	13.4	
2	19.4		7	13.4	
3	20.7		8	14.5	
4	18.6		9	15.1	
5	18.9		10	15.8	
6	20.6		11	17.0	
7	20.8		12	16.8	
8	20.0			—	—
9	19.2		13	15.4	711.5
10	19.3		14	15.0	
	—	—	15	14.7	
11	19.9	264.7	16	14.0	
12	20.5		17	14.0	
13	20.2		18	14.0	
14	19.1		19	14.5	
15	16.6		20	14.9	
16	14.9		21	13.5	
17	13.8		22	13.8	
18	13.7		23	13.4	
19	14.2		24	12.8	
20	14.8		25	12.5	
21	14.8		26	14.0	
22	13.6		27	14.4	
23	11.4		28	14.8	
	—	—	29	15.2	
24	10.0	472.2	30	16.0	
25	10.0		31	14.5	
26	9.6		Jan.		
27	9.6		1	14.6	
28	9.2			—	—
29	9.0		Total	—	997.5
30	9.7				

winter progressed. Examination of the second group indicated a survival of 46.9 percent or 98.9 percent of the Group 1 rate. A theoretical loss of 1.1 percent had occurred between October 31st and November 11th.

On November 24th the third group of eggs was removed, after 472 heat units. During the period since the previous removal, the stream flow remained stable but the temperature declined from a daily mean of 52 degrees F. to a mean of 42 degrees F. The third group showed a survival rate of 40.5 percent or 85.4 percent of the Group 1 rate. A theoretical 14.6 percent mortality had occurred from October 31st to November 24th.

On December 13th, the fourth group was removed, after 712 heat units. Since the previous removal, the Sacramento Valley had experienced severe storms which caused Mill Creek to flood. In certain parts of the experimental stream section boulders and gravel were piled 18 to 24 inches deep, while in other portions the stream bed was scoured bare by erosion. Information obtained from the California

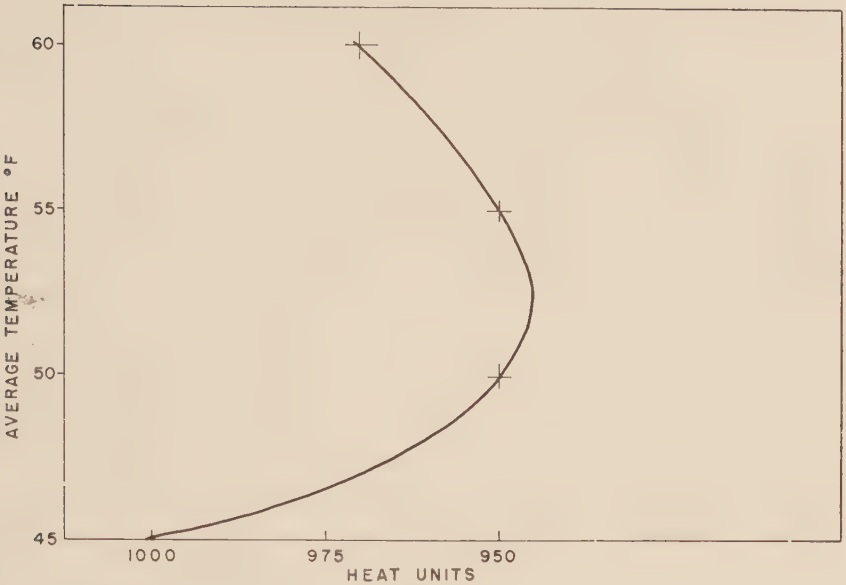


FIGURE 2. The estimated number of heat units required to hatch king salmon eggs at various temperatures.

State Division of Water Resources indicates that the stream flow increased on December 7th to 1,250 c.f.s. at a point 100 yards downstream from the planting site, which was an increase of 25 times the rate of flow recorded at the time the eggs were buried.

This high water caused a high loss to the eggs remaining in the stream bed. Only 17.4 percent of Group 4 survived, or 36.7 percent of the Group 1 rate. A loss of 63.3 percent had occurred since October 31st. Temperatures began at 41 degrees F. and rose during the period of the storms, remaining at approximately 47 degrees F. the remainder of the time Group 4 was in the stream.

A sufficient number of heat units had accumulated by the first part of January to permit removal of the fifth group of eggs. However, high water conditions prevailed (Figure 3), and the investigators were not able to work in the stream until the end of February.

The upper Sacramento River system continued to flood during the last stage of the experiment. The water gauge used by the California State Division of Water Resources was torn from its position by the flood. Records received from the Water Resources Branch of the United States Geological Survey show the flow of Mill Creek rose to 5,240 c.f.s., or approximately 100 times the flow recorded at the time the eggs were planted. The result was that all but six sacks of eggs disappeared from the stream bed. Examination of the sacks that could be found revealed that none of the embryos had survived the floods. The shifting of the channel and the eroding and smothering action of silt and sand apparently caused a complete kill of the developing young salmon.

Damage by silting and erosion has been reported by biologists previously. Allen (1951) describes the vulnerability of alevin to freshets. Davidson and Hutchinson (1943) observed pink salmon destruction

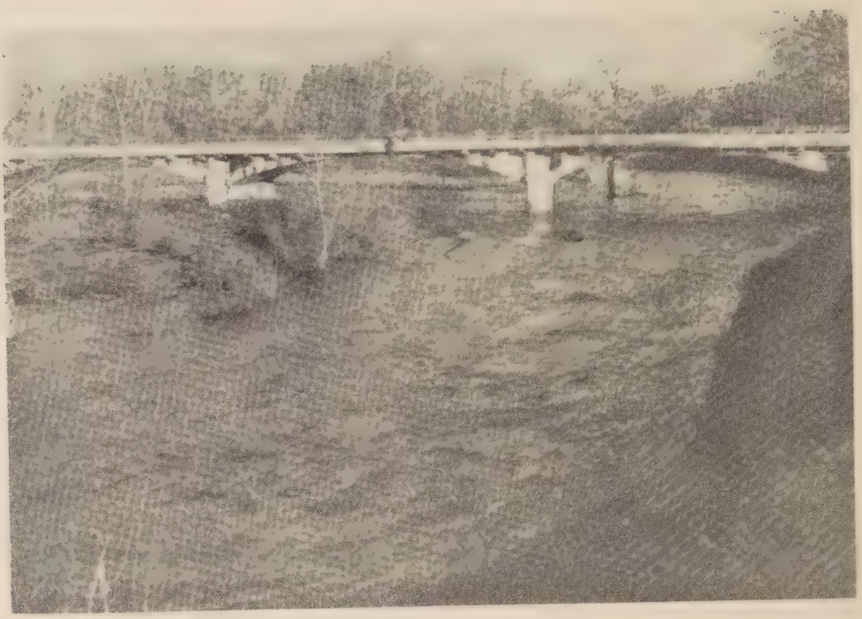


FIGURE 3. Stream flow at flood stage January 13, 1953, when the flow was approximately 1,500 c.f.s.

from floods in Alaska. Neave (1947) reported loss of chum salmon eggs by silting and suffocation in Nile Creek, British Columbia. Shapovalov and Berrian (1940) ran a silver salmon egg incubation experiment in hatchery troughs filled with gravel in which a loss of 89.8 percent resulted from silting.

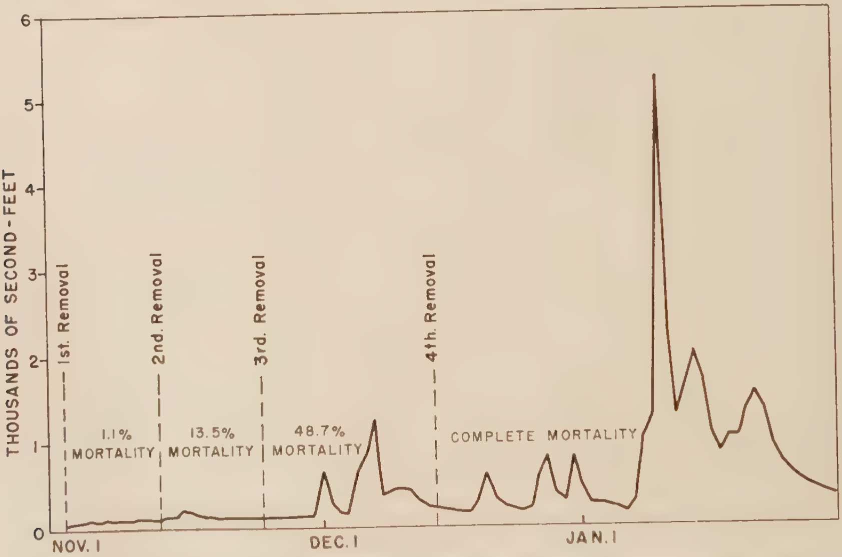


FIGURE 4. The fluctuations in stream flow of Mill Creek and the percentages of mortality of egg samples during the winter of 1952-1953.

Figures 4 and 5 show the stream flows and temperatures during the experiment. Sudden runoffs like the ones experienced in 1952 not only damage spawn in the gravel, but are likely to deprive future spawning salmon of proper spawning gravel. The unstable runoff pattern may well be the reason that only 1.79 percent of the Mill Creek stream bed was reported as suitable for spawning by Hanson, Smith, and Needham (1940).

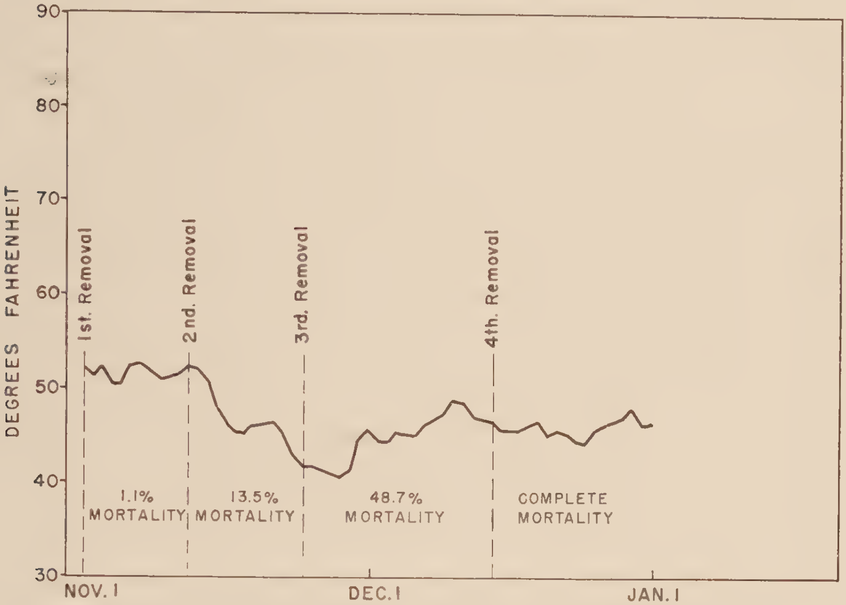


FIGURE 5. The fluctuations in temperatures of Mill Creek and the percentages of mortality of egg samples during the winter of 1952-53.

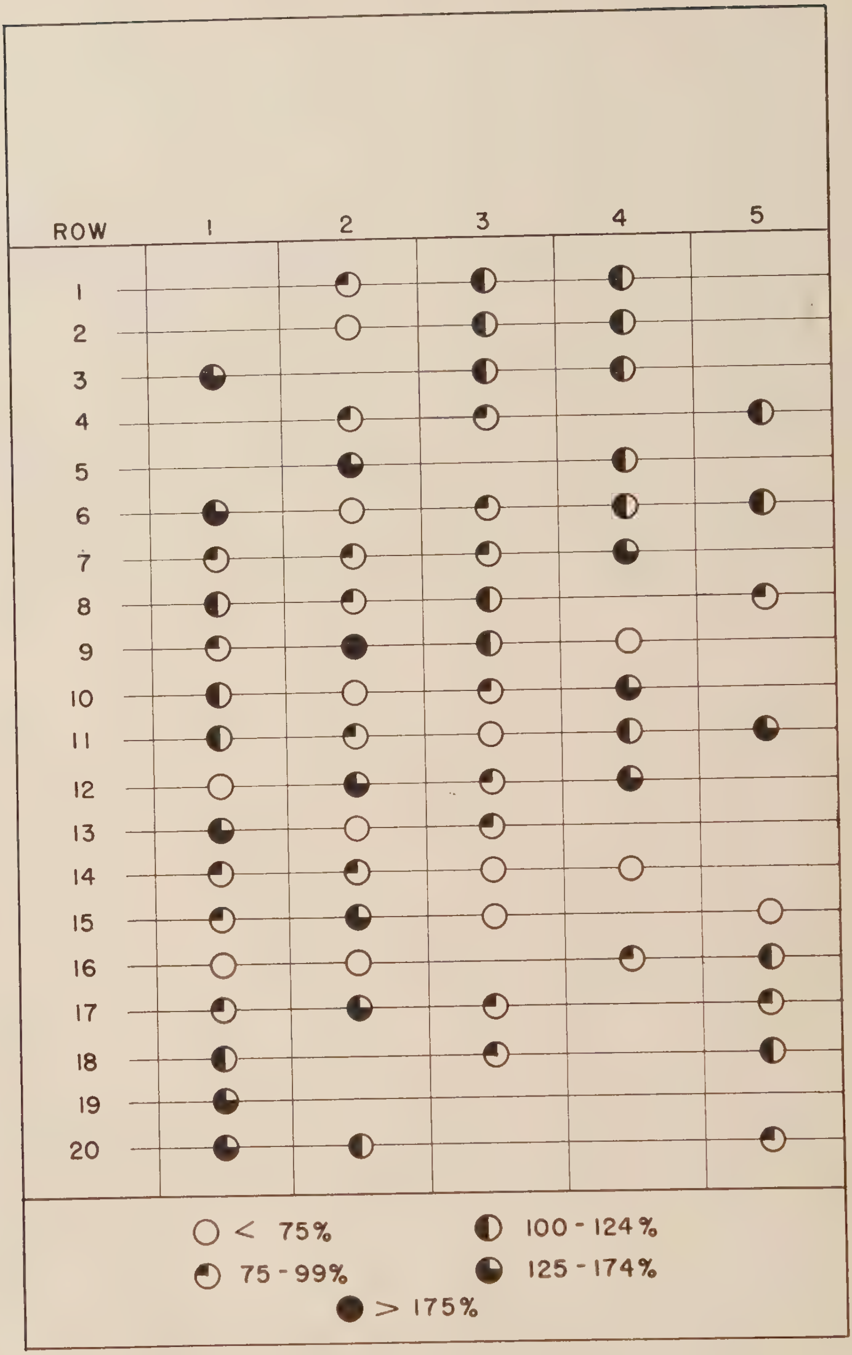
Influences of Position on Survival

The possibility that position in the stream might have significant influence on the rate of survival was considered. Within the 7- by 23-meter area selected for the experiment, a variation in velocity and in the direction of current existed. The greatest variation occurred between the fringe areas and the center of the stream.

The variation in survival was first reduced to a common denominator. This amounted to determining the average egg survival in each group and expressing the survival of each sack as a percentage of its removal group's average. It follows that any sack with better than average survival will be represented by a figure in excess of 100 percent.

The ratio of survivors in each sack compared to each group average was plotted in its relative position in the stream (Figure 6). It appeared that no group of eggs had any particular advantage over any others from the standpoint of position in the stream.

The variance of egg survival rates of each column was tested against all the other columns for each removal group. In addition to this, an



ROW	1	2	3	4	5
1		◔	◐	◐	
2		○	◐	◐	
3	◕		◐	◐	
4		◔	◔		◐
5		◕		◐	
6	◕	○	◔	◐	◐
7	◔	◔	◔	◕	
8	◐	◔	◐		◔
9	◔	●	◐	○	
10	◐	○	◔	◕	
11	◐	◔	○	◐	◕
12	○	◕	◔	◕	
13	◕	○	◔		
14	◔	◔	○	○	
15	◔	◕	○		○
16	○	○		◔	◐
17	◔	◕	◔		◔
18	◐		◔		◐
19	◕				
20	◕	◐			◔

○ < 75%
◔ 75 - 99%
◐ 100 - 124%
◕ 125 - 174%
● > 175%

FIGURE 6. Relative survival based on group averages of samples of eggs planted in gravel nests in Mill Creek.

analysis variance within the columns was made. No difference existed in survival rates among or within the columns of any group at the 5 percent level of significance.

No significant difference at the 5 percent level was found among the mean survival rates of the groups removed from the gravel on October 31st, November 11th, and November 24th. However, the mean survival rate of the group that was removed on December 13th was found to be significantly less than the means of the first three groups. The group removed on February 26th was not included in the analysis because of insufficient data for that group.

SUMMARY

One hundred sacks of eggs of king salmon (*Oncorhynchus tshawytscha*) were planted in the stream bed of Mill Creek, a tributary of the Sacramento River, California, in 1952. The sacks were removed 20 at a time at intervals during the period up to hatching stage to determine when mortalities occurred. In addition, temperatures and stream flows were recorded and other pertinent information was noted, to determine the cause of the mortalities.

Water flow was stable during the period when the first three groups of eggs were in the stream. The survival rates of these groups were not significantly different.

Between the times of the third and fourth removals, stream flow reached a maximum of 1,250 c.f.s. The average egg survival in the fourth group was less than half the survival of the third group. The increased mortality was attributed to erosion and silting.

High water conditions during January and February delayed removal of the last group of eggs. When the stream subsided, less than one-third of this group of sacks was found. Complete mortality had occurred during this period when the water flows had exceeded 5,000 c.f.s.

The influence of position on the survival of eggs was tested and found to be not significant.

Water temperatures remained well within the critical limits for salmon eggs during the entire course of the experiment.

Although the information available from this experiment is not conclusive, it does suggest a direct relationship between floods and mortalities of king salmon eggs.

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FISHES OF THE FAMILY PERCOPHIDIDAE FROM THE COASTS OF EASTERN UNITED STATES AND THE WEST INDIES, WITH DESCRIPTIONS OF FOUR NEW SPECIES

By Isaac Ginsburg

Fishes of the family Percophididae from the coasts of eastern United States and the West Indies have, to my knowledge, hitherto been recorded under one name, (*Hypsicometes*) *Bembrops gobioides* (Goode). Four new species are added here, making a total of five species divided into two genera. Specimens of all five species have been preserved in the collection of the U. S. National Museum for some time, where they have been cataloged as *gobioides*. Adequate samples of two species that appear to be common offshore in the Gulf of Mexico have been collected during recent years by the U. S. Fish and Wildlife research boats *Pelican* and *Oregon*. This added material made it possible to determine and distinguish these two species satisfactorily and aided in the proper distinction of the other species. Three of the four new species were obtained by the *Caroline* of the Johnson-Smithsonian Expedition. Specimens of two of the latter species were also collected by the *Albatross*, 68 and 69 years ago; they were identified as *gobioides* by Goode and Bean and were included in their account of that species as noted below.

Family PERCOPHIDIDAE

CHARACTERS COMMON TO THE FIVE SPECIES HERE TREATED: Notably elongate, slender. Head and anterior part of body depressed, the width in relation to the depth gradually decreasing from head backward, becoming somewhat compressed at caudal peduncle; ventral aspect flat, especially anteriorly, forming a nearly horizontal plane. Snout notably depressed, flat, broad, rounded anteriorly, somewhat ducklike. Hard part of upper jaw with a narrow emargination on upper surface at symphysis, producing a bilobate effect on a dorsal view, the small space between the lobes more or less bridged with a yellowish, moderately soft tissue. Nostrils small or moderate; one behind the other on a horizontal approximately through upper margin of pupil, at some distance in front of eye; close to each other or rather widely spaced, depending on the genus; anterior one with a slightly raised rim; posterior one with a well raised, somewhat tubular rim, hind part of tubule higher. A lengthwise mucous channel dorsad of the nostrils, opening by two pores of variable size, one at its anterior end not far from upper jaw, the other at some distance from its posterior end, near posterior nostril. Mouth rather large, nearly horizontal, superior, lower jaw extending beyond upper. Eyes large, interorbital narrow. Mandibular rami notably expanded, placed in a ventral position. Maxillary reaching to under posterior margin of pupil or a little behind. Teeth in bands on jaws, vomer, and palatines, the band in upper jaw broadening at symphysis; some inner teeth of vomer, of palatines, and at symphysis of upper jaw moderately enlarged in some species. Gill cover having its posterior and greater part thin and flexible, somewhat tapering and prolonged posteriorly, its upper margin horizontal and free for a considerable distance, its lower margin sharply oblique, running upward and backward; with three moderate spinous points, the upper spine close to upper margin, the middle spine moderately spaced, the two forming apical points of two moderate or slight ridges converging forward, the lower spine widely separated, placed at lower margin of gill cover and constituting part of subopercle. Preopercle with one to three spinous points at angle present or absent (subject to individual variability). Gill opening wide, branchiostegal membranes overlapping under anterior margin of eye or a little more forward. Gill rakers in moderate numbers or rather numerous. Pseudobranchiae well developed. Scaled nearly all over, including head, chest, fleshy pectoral base, and mandibular rami; snout scaled posteriorly, incompletely scaled to nearly scaleless anteriorly; anterior space between mandibular rami scaleless except in *Chriomystax squamentum;* pelvic and pectoral fins scaled on a small area near base, scaleless in larger part; caudal scaled on a larger area near base; dorsal and anal scaleless; scales on sides of body moderately ctenoid, others cycloid, at least in large part. (The scalation is incomplete or nearly all missing in almost all specimens examined and not all details are accurately determinable; consequently, the above statements might be subject to a moderate revision.) Lateral line beginning at upper angle of gill opening, running horizontally over upper margin of opercle, curving directly behind head, except in individual variants of *Bembrops anatirostris* (p. 636), and dipping rather sharply down, posterior end of curve approximately at end of pectoral, thence running nearly straight backward and nearer to lower than upper profile. First dorsal with six flexible spines (the count constant as determined in 124 specimens of all five species). Second dorsal with 14–18 rays, all segmented; anal similar to second dorsal, with 17–19 segmented rays; the rays in the two fins notably well spaced. Pelvic horizontally placed on ventral aspect of abdomen, its base well in advance of pectoral, approximately under preopercular margin, its end falling considerably short of anus; with one flexible spine rather well developed and five segmented rays. Pectoral extending moderately behind a vertical through anal origin, with 22–28 rays. (Caudal damaged in nearly all specimens examined; seems to be moderately emarginate with the rays near the upper margin somewhat longer than the corresponding lower rays.)

METHODS OF STUDY: The dorsal and anal fins are very often damaged, many of the rays being broken off, leaving only a short stump. However, the rays are widely separated and readily countable even when damaged and in the small specimens. The last ray is split to its base and the two branches have been counted as one ray.

The scales are deciduous and most or nearly all of them are missing in almost all specimens examined. However, when the scales are missing their pockets are prominently outlined. The counts of the scales here given generally refer to the number of oblique rows of scale pockets, beginning with the row that is wholly or partly behind the short, rather sharp spine at the upper anterior angle of the gill opening and ending at the caudal base. Some of the counts here recorded may be off by one or two scales, especially for specimens on which part of the count was made of the rows of actual scales and part of the rows of pockets, or in case of specimens having the rows somewhat irregular in places. But, on the whole, the counts made closely approach the true numbers.

The gill raker standing squarely within the angle of the arch is the longest, and it has one "root" on the upper limb and one on the lower. Following my usual procedure, it has been uniformly included in the count of the lower limb. The tuberclelike outgrowths at both ends of the arch, when present, have been included in the gill raker count as discussed under *Bembrops*.

The given length of the pectoral fin and the pelvic fin is that of the longest ray, from its point of articulation; that of the caudal from end of hypural to tip of longest ray, which is located at upper margin of the fin. The depth was measured at the origin of the first dorsal. The measurement of the "peduncle" refers to the least depth of the caudal peduncle. The head was measured from the apex of the lobe on the snout (not the middle anterior point) to the posterior margin of the flexible opercle. The snout was measured from the same anterior point as the head to the anterior soft margin of the eye. The eye measurement represents the horizontal distance between its soft margins. Numerical values of proportional measurements are expressed as a percentage of the standard length unless otherwise stated.

Specimens examined: This study is based chiefly on the western Atlantic specimens of this family in the collection of the U. S. National Museum and the museum catalog numbers are given under the accounts of the species. In addition, the types of *Chrionema chryseres* and *C. squamiceps* that Gilbert described from off Hawaii have been examined for comparative purposes as discussed below. Also, single specimens of four other species of the genus *Bembrops* from the Pacific and Indian Oceans were examined and some of their characters are discussed under the account of that genus.

Brazilian species: Two percophidid species are known from the coast of Brazil, from which the marine fish fauna has much in common with the regions here considered. One species, *Percophis brasiliensis* Quoy and Gaimard, a notably long and slender fish, is readily distinguishable by its much more numerous fin rays (D IX; 31. A 41 in one specimen, USNM 77325) and other well marked characters. The other species, *Hypsicometes heterurus* Miranda Ribeiro (1915, pls.), of which no specimens are available for examination, is described as having the following combination of characters: D VI; 14. A 17. P 25; lateral line about 59; eye 1½ times in snout. The combination of the given counts is close to that of the species here designated as *Bembrops macromma*, but the eye is smaller than in that species. Miranda Ribeiro's photograph shows that the anterior straight part of the lateral line extends for some distance behind the head, which, except in individual variants of *B. anatirostris*, is different than in the specimens examined of the species treated here.

Nomenclature: The question of what family name to apply to the two genera here considered is one of biology rather than of mere nomenclature. The problem is how the genera *Bembrops*, *Chriomystax*, and their near relatives are to be classified into families and how to determine the proper limits between the families. The two genera mentioned fall into the larger groups that Regan designates as Trachiniformes and Jordan as Percophidiformes.

Regan (1913, pp. 140–144), subdivides his "Division 10. Trachiniformes," which is a subordinate category in his "Suborder Percoidea" and apparently roughly corresponds to the superfamily category of other taxonomists, into 13 families, 9 of which contain only 1–3 genera each. However, such splitting of the relatively few, seemingly more or less related genera into an excessive number of families is not based on an adequate comparative study of their morphology; at least such a study is not included in the published record. After an examination of the external characters of a number of the genera concerned, it seems that Regan's family category as applied to these fishes is equivalent to the category designated as subfamily or even tribe by other modern taxonomists, or, in other groups, by Regan himself.

A classification published later by Jordan (1923, pp. 228–231) agrees in the main with that of Regan. Jordan likewise divides these genera among many families. But the two classifications differ in some particulars, two of which may be mentioned here: Jordan also groups the families into a next higher category which he calls "Series" that corresponds roughly with Regan's "Division," but the families that Regan includes in his Trachiniformes are placed by Jordan in four "Series;" and, in some instances, Jordan shuffles the genera from one family to another so that the content of some families is different from that of Regan. These differences cast some doubt on the adequacy of both classifications.

The genera that are of immediate concern in this paper are placed in three families in both classifications, but the genera are differently distributed and the two authors use different names for one of the families. Both recognize the family Percophididae with one genus, although Regan does not expressly state so. Besides that family, Regan recognizes the Bembropsidae with two genera, *Bembrops* and *Chrionema*, and the Hemerocoetidae with *Hemerocoetes* and *Acanthaphritis*. He also indicates that *Pterosaron* Jordan and Snyder is the same as *Acanthaphritis* Gunther. This suggested synonymy is open to question.

In Jordan's classification, the Hemerocoetidae includes only the type genus; while the third family, which is designated Pterosaridae instead of Bembropsidae, contains *Bembrops*, *Chrionema*, *Acanthaphritis*, *Pterosaron*, and *Osopsaron*. The last-named genus is possibly the same as *Acanthaphritis*, while the other two genera placed by Jordan in his Pterosaridae, *Hypsicometes* Goode and *Bathypercis* Alcock, are presumably synonyms of *Bembrops*.

The six or seven genera discussed above, which evidently are of close relationship, are placed in three families and the content of two of these families differs in the two classifications. If this process of splitting the families is carried to its logical conclusion, four families should be recognized for the following four diverging groups of genera: *Percophis*, *Bembrops* and *Chrionema*, *Acanthaphritis* and *Pterosaron*, and *Hemerocoetes*. Such excessive splintering of the families seems out of line with family divisions in other groups of fishes and in zoology in general and serves no useful purpose. Therefore, it would seem best to place all these genera in one family. At any rate, the terminology used in this paper is in line with this viewpoint. Perhaps other related genera should be included in the Percophididae.

Key to five Western Atlantic percophidid species

1a. Maxillary without a tentacle. Anterior part of space between mandibular rami scaled. Caudal without a definite spot behind its base. Gill rakers 7–9+20–21, those at the ends slender, moderately developed. Pectoral rays 21–22. Dorsal rays usually 15, sometimes 16. Scales 55–61. **Chriomystax squamentum** (p. 629)

1b. Maxillary with a broad tapering tentacle. Space between mandibular rami scaleless. The smaller specimens with a caudal spot disappearing with growth (unknown for *macromma*). Gill rakers 4–6+14–16, including 1–4 at both ends of arch in form of low tubercles.

- *2a.* Scales 47. Pectoral rays 24. Dorsal rays 15. Eye larger than snout. **Bembrops magnisquamis** (p. 633)
- *2b.* Scales 55–59. Pectoral rays 25. Dorsal rays 14. Eye subequal to snout, varying slightly both ways (well divergent in this character from *anatirostris* and approaching *gobioides*, see table 4). Without a prolonged dorsal spine in three males examined (185–202 mm.). A lateral series of four spots . . . . **Bembrops macromma** (p. 634)
- *2c.* Scales 61–71. Pectoral rays 26–28. Eye smaller than snout.
  - *3a.* Dorsal rays usually 15, sometimes 14. The larger males having the second dorsal spine filamentous. With a lateral row of about 10 spots better marked in the smaller specimens. **Bembrops anatirostris** (p. 635)
  - *3b.* Dorsal rays usually 17, sometimes 18. Without a filamentous dorsal spine. Without a definite lateral row of spots. **Bembrops gobioides** (p. 637)

Chriomystax, new genus

GENOTYPE: *Chriomystax squamentum*, new species.

COMPARISON: *Chriomystax* agrees with *Chrionema* Gilbert (genotype *Chrionema chryseres* Gilbert (1905, p. 645) by original designation) in lacking a maxillary tentacle, the presence of which is a constant feature of *Bembrops*. *Chriomystax* differs from *Chrionema* in having the ventral aspect of the head, that is, the mandibular rami and the space between them, scaled instead of naked. (In the species of

Bembrops examined the mandibular rami are more or less scaled, but the area between them is naked.) *Chriomystax* further differs in having 18 anal rays, instead of 24 as in *Chrionema chryseres*. The latter character ordinarily, in fishes in general, would not be deemed of generic importance. However, in the species of the two genera here treated the number of anal rays varies intraspecifically and differs interspecifically within comparatively narrow limits. In eight species of *Bembrops* and two of *Chriomystax* the total range is 16–19 (see table 1 and the counts of extralimital species, p. 632). Consequently, it seems that in this family this difference sometimes indicates a higher degree of divergence than that of species.

Chrionema chryseres, the type species of its genus, differs in three other characters: The gill rakers are fewer and those at both ends of the arch are much reduced, in the form of low tubercles, while in the two species of *Chriomystax* in addition to being more numerous in total count, those at the ends of the arch are slenderer and longer, not in the form of tubercles; the bands of teeth are conspicuously wider in *C. chryseres;* and it is a much rougher fish, the scales being more strongly ctenoid. However, any one or all three of these differences might possibly be governed by growth, the single available specimen of *C. chryseres* being considerably larger, 181 mm. in standard length, while the two species of *Chriomystax* examined are 29–55 mm. in the same length.

In the original account of his *Chrionema*, Gilbert (1905, pp. 645–646) included two species—*chryseres*, the genotype, and *squamiceps*. The latter species is near *Chriomystax squamentum* in its structural characters and should be placed in the same genus with it. The differences between these two congeneric species are discussed below.

***Chriomystax squamentum*, new species**

Description: D VI; 15–16. A 18. P 21–22. Sc 55–61. GR 7–9+20–21. Dorsal rays usually 15, sometimes 16. Anal rays constantly 18. Pectoral rays 21–22. (The uppermost pectoral ray has a slight ridge along its upper aspect that may be separated cleanly when some pressure is applied to it with a dissecting needle, and it then appears like a very thin distinct ray. However, the ridge does not seem to be separated basally from the ray. It apparently does not represent a separate ray and was not included in the count of the pectoral rays.) Gill rakers at both attached ends of the outer arch slender, graduated, not in the form of short stumpy tubercles, except one short gill raker, abruptly shorter than the others, intermediate in development between a gill raker and a tubercle, occasionally present at either end of the arch; gill rakers, including the short one when present, 7–9+20–21 or 27–30 in total number on both limbs. Anterior area between mandibular rami covered with imbricated cycloid scales. Posterior pore of lengthwise mucous channel on snout placed between the two rather widely separated nostrils.

Measurements of two specimens, including the holotype, 53.2–55.3 mm. in standard length, the caudal and pectorals damaged: pelvic 20.0–21.5, depth 14.3–14.7, peduncle 5.2–5.6, head 36.0–36.5, maxillary 13.4–13.9, snout 9.4–10.0, eye 11.8–12.7; snout 0.71–0.74 as long as eye.

Body with a lengthwise, nearly median row of eight rather diffuse spots, the first a little behind pectoral base, the last at caudal base; the second spot largest and most prominent, rounded, elongate with its longer axis longitudinal, centered approximately over anal origin; some irregular smudges over median row, very diffuse; two diffuse smudges on caudal, at its base, at upper and lower margin; no well marked spot on caudal at some distance behind its base and no other prominent markings.

Table 1.—*Frequency distribution of the number of dorsal, anal, and pectoral rays in five Western Atlantic percophidid species*

Species	*Dorsal rays*					*Anal rays*			*Pectoral rays*							
	14	15	16	17	18	17	18	19	21	22	23	24	25	26	27	28
Chriomystax squamentum		25	3				28		17	11						
Bembrops magnisquamis		2				2						2				
B. macromma	3						3						3			
B. anatirostris	4	37				8	33							7	30	4
B. gobioides				49	2	2	45	4						6	36	8

In small specimens, every spot in the median row is made up of very small, black, somewhat stellate spots. Another row of small, rounded, rather crowded, almost solidly bluish black spots above the median row, every spot with many very fine radiating lines, presenting a stellate appearance in gross effect. Two rows of similar but somewhat smaller spots below the median row. The two spots on caudal, at its base, likewise in form of two groups of very small spots, the groups somewhat confluent. The juvenile color pattern is present in specimens about 29–32 mm. in standard length, while the pattern of the larger specimens is described above from specimens 30–55 mm. in the same length.

Holotype: USNM 108394. *Caroline* Sta. 102; lat. 18°51′ N., long. 64°33′ W.; off Virgin Islands, 140 fathoms; Mar. 4, 1933; 53.2 mm. in standard length.

Paratypes: 27 specimens, 29.3–55.3 mm. in standard length, taken at same station as holotype; the caudal damaged in all specimens (USNM 108393, 108396).

Comparison: This species is near (*Chrionema*) *Chriomystax squamiceps* (Gilbert, 1905) from Hawaii, agreeing with it in its structural characters, including the presence of scales between the mandibular rami. The holotype of *squamiceps* was examined and its counts are as follows: D VI; 16. A 18. P 23. Sc 66. GR 7+20. Therefore, the Atlantic species here described differs in having fewer scales and pectoral rays. Possibly it will also prove to average fewer dorsal rays.

Etymology: The name *squamentum* is a contracted form of squamimentum (scaled chin).

Genus *Bembrops* Steindachner

Bembrops Steindachner, Icthyologische Beiträge, (V) p. 163, 1876 (genotype *Bembrops caudimacula* Steindachner, by monotypy).

Hypsicometes Goode, Proc. U. S. Nat. Mus., vol. 3, p. 347, 1880 (genotype *Hypsicometes gobioides* Goode, by monotypy).

Description: Maxillary with a broad tentacle at its end, of moderate length, its base nearly as wide as maxillary, tapering. Space between mandibular rami scaleless. The smaller specimens having a spot on the caudal near its base, nearer to upper than lower margin, disappearing with growth (not determined for *macromma*). The two nostrils rather close together, as compared with *C. squamentum*. Posterior pore of lengthwise mucous channel on snout close to and slightly dorsad of posterior nostril.

Table 2.—*Frequency distribution of the number of oblique rows of scales over lateral line in five Western Atlantic percophidid species*

Species	*Scales*																		
	47		55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71
Chriomystax squamentum			2	3	6	3	1	1	2										
Bembrops magnisquamis	1																		
B. macromma			1			1	1												
B. anatirostris									2	5	3	5	8	13	3		1		
B. gobioides										1	5	7	9	11	8	3	3	1	1

The gill rakers in *macromma*, *anatirostris*, and *gobioides* are as follows. The upper limb of the outer gill arch has two graduated gill rakers at the angle and usually two tuberclelike outgrowths at the attached end. One outgrowth in between varies in its development. At one extreme it can be classed with the tubercles and at the other it may be taken to represent a short gill raker; and it occurs in all degrees of development in between the extremes. On the lower limb the gill rakers decrease in length from the one on the angle (here included in the count of the lower limb) forward. At the attached end 1–4 tubercles occur that are similar to those of the upper limb, and the outgrowth behind the tubercles varies in development in a similar manner as the corresponding one on the upper limb. As the number of tubercles is readily determinable and no sharp line can be drawn between them and the gill rakers, all are included in one count in this comparative study.

In one small specimen each of *anatirostris* and *gobioides*, 58 and 43.5 mm. standard length, respectively, the gill rakers near both ends of the arch are relatively better developed and sharply delimitable from the two tubercles at both ends. Therefore, the relative development of the gill rakers as compared with the tubercles appears to change with growth, in these two species anyway.

Development in the two available specimens of *magnisquamis* (p. 633) is somewhat different than in *macromma*, *anatirostris*, and *gobioides*. Although an adequate sample is not available to determine growth changes satisfactorily, it seems that in the latter three species the anterior gill rakers are not in the form of tubercles in small fish, and one at both ends changes to a tubercle with growth.

Table 3.—*Frequency distribution of the number of gill rakers, including tubercles, in five Western Atlantic percophidid species*

Species	*Upper limb*						*Lower limb*						*Total both limbs*								
	4	5	6	7	8	9	14	15	16		20	21	18	19	20	21		27	28	29	30
Chriomystax squamentum				10	4	1					8	7						6	6	2	1
Bembrops magnisquamis	1	1					2						1	1							
B. macromma		3					3							3							
B. anatirostris	1	39	1				4	31	6				1	3	30	7					
B. gobioides	3	48					13	29	9				2	12	28	9					

Extralimital specimens examined: Counts of four extralimital specimens in the U. S. National Museum, examined for comparative purposes, are as follows. Taken off Kagoshima, Japan, now labeled as *Bembrops maculicauda* (59647, 134 mm.): D VI; 14. A 16. P 24. Sc 52. GR 4+13. Holotype of *B. filifera* Gilbert from off Hawaii (51613): D VI; 14. A 18. P 27. Sc 63. GR 4+15. Holotype of *B. filifer* Fowler from east of Masbate Island, Philippines (98866): D VI; 14. A 16. P 28. Sc 51. GR 5+14. Paratype of *B. nematopterus* Norman from off Zanzibar (109489): D VI; 14. A 16. P 25. SC 47. GR 5+15. While it is necessary to study adequate samples to determine the intraspecific variability of these species, the combinations of the foregoing counts as compared with those of the five Western Atlantic species given in tables 1–3 show that the extralimital species examined are different. Also, in three of these species, excluding *caudimacula*, the first spine is filamentous and prolonged, while among the Atlantic species only *anatirostris* is now known to have a prolonged dorsal spine, and in that species it is the second instead of the first spine that is prolonged in large males.

Bembrops magnisquamis, new species

Description.—D VI; 15. A 17. P 24. Sc 47. GR 4–5+14. Fin ray counts the same in both available specimens. Scales in 47 rows over lateral line in holotype; some scales missing in paratype and number not definitely determinable, but approximately the same. Anterior gill rakers in the smaller specimen (paratype) short, slender, graduated, not tuberclelike; in larger specimen end outgrowth on upper limb a low tubercle, anteriormost one on lower limb intermediate in development.

Table 4.—*Frequency distribution of the numerical value of the measurement of the snout divided by that of the eye in three Western Atlantic species of* Bembrops, *segregated in size groups*

Species	*Standard length in mm.*	*Ratio*							
		0.9	1.0	1.1	1.2	1.3	1.4	1.5	1.6
anatirostris	58–115			1	3	2			
gobioides	81	1							
anatirostris	117–146				2	1	2		
gobioides	123–145			3					
macromma	154–168	1	1	1					
anatirostris	154–180					3	3		
gobioides	162–181				5	2			
anatirostris	186–221					1	8	5	
gobioides	183–224			8	21	8			
anatirostris	231–271					1	4	4	1

Following are the proportional measurements of the holotype and paratype, respectively (caudal, pectoral, and pelvic damaged in both specimens): Depth 14.5, 13.5; peduncle 6.3, 6.0; head 36, 34; maxillary 14.5, 13.3; snout 10.2, 8.9; eye 10.5, 9.6.

First dorsal with a large subtriangular black spot at its base extending from first interspinal membrane to fifth spine, a whitish area above spot, anterior produced part above whitish area again black; a similar smaller black spot at base of second dorsal from first interradial membrane to third ray; in gross effect the two spots appearing partly ocellated above (described from the holotype). The specimen appears to be now largely faded, but the following marks are more or less faintly evident: A dusky transverse bar on upper half of caudal at its base; a better marked spot on midline below bar; an elongate narrow, short, dusky band behind the transverse bar in the approximate position of the caudal spot usually present in the smaller specimens of the species of *Bembrops;* three short elongate bands on mid-dorsal line in front of first dorsal; anal with blackish margin. The paratype has the spot on the first dorsal reduced, the transverse bar on the caudal very faint, and a few black scattered points on peduncle; otherwise it seems faded.

HOLOTYPE: USNM 45985. *Albatross* Sta. 2134; lat. 19°56′06″ N., long. 75°47′32″ W.; off Santiago, Cuba; 254 fathoms; Feb. 27, 1884; 85.5 mm. in standard length.

PARATYPE: *Caroline* Sta. 99; lat. 18°14′ N., long. 64°51′ W.; 220 fathoms; off Virgin Islands, Mar. 3, 1933; 50 mm. in standard length (USNM 108395).

COMPARISON: This species is easily distinguishable from the other four Western Atlantic species treated here by its large scales. The predominant number of anal rays in the other four species is decidedly 18, while in the two available specimens of this species the number is 17. It has, or at least averages, fewer pectoral rays than the three Western Atlantic species of *Bembrops.* The gill raker count averages rather low, comparatively.

Bembrops macromma, new species

DESCRIPTION: D VI; 14. A 18. P 25. Sc 55–59. GR 5+14. Dorsal, anal, and pectoral rays and combined number of gill rakers and tubercles constant in the three specimens examined.

Measurements of three specimens 185–202 mm. (154–169 mm. in standard length): Caudal 20.0–21.5, pectoral 23.5–24.5, ventral 17.0–18.5, depth 13.8–14.8, peduncle 5.5–6.2, head 37.5–38.5, maxillary 14.6–14.9, snout 10.5–11.1, eye 10.6–11.3; ratio of snout divided by eye 0.9–1.1.

A series of three large, diffuse, dusky spots, equally spaced, the first over anus, the third under end of dorsal fin; the first placed just below lateral line, the other two just above it; each of the two interspaces between the spots with two rather faint transverse dusky bands more or less developed; a fainter and smaller spot on caudal peduncle at base of caudal fin in a line with the above three somewhat more prominent spots; three faint smudges at dorsal profile over interspaces of the four median spots; anterior part of the first dorsal to the third spine black for entire height of fin, posterior part abruptly light, without pigment (in one specimen a small black spot at base of fin behind third spine); anal whitish, broadly margined with black; other fins more or less dusky, especially distally.

Holotype: USNM 108392. *Caroline* Sta. 81; lat. 18°35′30″ N., long. 65°23′54″ W.; off Virgin Islands, 300 fathoms; Feb. 26, 1933; 186 mm., 154 mm. in standard length.

Paratypes: *Caroline* Sta. 100; lat. 18°40′15″ N., long. 64°50′15″ W., off Virgin Islands, 150 fathoms; Mar. 4, 1933; 2 specimens, 185–202 mm. (USNM 108391).

Comparison: In general appearance, as compared with *anatirostris* and *gobioides*, this species seems to be a somewhat more compact fish, not as slender as its two near congeners, with a shorter snout, larger eye and somewhat different color pattern. Differences in the proportional measurements of the depth of the body and caudal peduncle do not show up well even in the few specimens measured (compare accounts of the species). As the eye is larger and the snout shorter, at least on the average, in this species than in the other two, the numerical value of the ratio of the snout divided by the eye for all three species is given in table 4. When specimens of approximately like size are compared (table 4), *macromma* differs from both species, the extent of divergence being greater when compared with *anatirostris*. This species has lower counts of scales and pectoral and dorsal rays, at least on the average, than the other two species (tables 1, 2). In the number of dorsal rays it intergrades with *anatirostris*, but is well distinguished from *gobioides*. Taking all the marked structural differences and the color pattern into consideration, it is not difficult to distinguish *macromma* from *anatirostris* and *gobioides*. Its distinction from the other two Western Atlantic percophidid species is indicated under their accounts. It is compared with *Hypsicometes heterurus* Miranda Ribeiro on page 626.

***Bembrops anatirostris*, new species**

Description: D VI; 14–15. A 17–18. P 26–28. Sc 61–69. GR 4–6+14–16. Dorsal and anal rays usually 15 and 18, often 14 and 17, respectively. Pectoral rays with the mode at 27, varying 26–28. Gill rakers, including the 1–4 tubercles at both ends of the arch, nearly always 5 on upper limb, infrequently 4 or 6, modally 15, varying 14–16 on lower limb; usually 20 in combined number on both limbs, varying 18–21. The larger males having the second dorsal spine filamentous, considerably prolonged, reaching base of second dorsal ray in one male 177 mm., base of fourth to sixth ray in six males 195–250 mm., base of sixth to ninth ray in six males 250–315 mm., not prolonged in 7 males 185 mm. or less. (This development is not present in *B. gobioides*, of which a good composite sample was examined. It is also not present in the specimens examined of the other three percophidid species treated here, but the available samples are not adequate for a final determination of this point in the latter species.) Lateral line sloping downward directly behind posterior margin of head or continued horizontally and beginning to slope at some distance behind head (only species having variants showing the latter conditions, both variations sometimes shown on the two sides of the same specimen).

Measurements of five specimens 241–261 mm. in standard length and five specimens 142–167 mm. in same length, the latter in parentheses: Caudal 19.5 in 1 (22 in 1), pectoral 21.0–22.5 (22.0–23.5), pelvic 14.2–15.7 (15.1–16.2), depth 12.7–14.2 (12.8–14.7), peduncle 5.0–5.8 (5.0–5.7), head 38.5–41.5 (36–37), maxillary 14.2–16.0 (14.2–14.6), snout 12.5–13.2 (11.3–12.2), eye 8.1–9.7 (8.4–8.9). The ratio of the eye in the snout is shown in table 4.

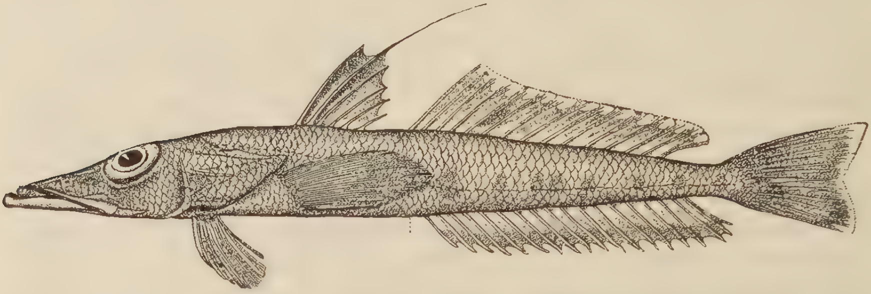

FIGURE 120.—*Bembrops anatirostris*, from a paratype (USNM 157735) 261 mm. in standard length, about 315 mm. long, from off Cape San Blas, Fla. (Drawn by Mildred H. Carrington.)

With a lengthwise, somewhat irregular row of about 10 diffuse irregular spots running along lateral line and continued forward under its anterior arch; the spots of various sizes and shapes and irregularly spaced, some of them doubled; fleshy pectoral base and anterior part of opercle with a silvery wash; anal whitish with a supramarginal blackish band; other fins more or less dusky, the pigment somewhat better developed distally; filament of second dorsal spine in male black.

HOLOTYPE: USNM 155470. *Pelican* Sta. 9; lat. 29°02′ N., long. 88°45′30″ W.; east of the Mississippi Delta; 170 fathoms; male 235 mm. in standard length, the caudal damaged, approximately 284 mm. long.

PARATYPES: 11 specimens 117–245 mm. in standard length obtained with the holotype (USNM 155471). Also, 29 specimens 58–271 mm.

in standard length, approximately 71–327, mm. long, obtained in 60–200 fathoms by the *Oregon*, the *Caroline*, and the *Albatross* off the following localities: Tampa (USNM 157734), Cape San Blas (USNM 44609, 157735, 157738) and Pensacola (USNM 157736–7, 157739–40), Fla.; Chandeleur Islands, La. (USNM 45976); Mississippi Delta (USNM 157733); Puerto Rico (USNM 117867–8).

Comparison: This species is near *gobioides*. The chief character that proves the distinctness of the two species and the one that is most useful in separating them refers to the number of dorsal rays, usually 15 or 17, sometimes 14 or 18, in *anatirostris* and *gobioides*, respectively (table 1). This difference seems to be absolute, as in 92 specimens of both species examined not one had 16 rays. This species also differs from *gobioides* in having the second dorsal spine of large males filamentous and in the presence of a lateral row of spots. On the average, the snout is longer and the eye smaller in *anatirostris*. The two species diverge considerably in the numerical value of the ratio of the eye in the snout (table 4) when specimens of approximately like size are compared, but they intergrade in this character.

Populations: The two specimens from Puerto Rico examined have the gill raker count near the upper limit of the range of distribution of the rest of the specimens, which were taken on the coast of the United States, while that of the scale count is near the lower limit of the range of the United States specimens, namely, GR 5+16, Sc 62, in both specimens from Puerto Rico. The counts of these two specimens are included in tables 2 and 3.

Bembrops gobioides (Goode)

Hypsicometes gobioides Goode, Proc. U. S. Nat. Mus., vol. 3, p. 348, 1880 (off Long Island, N. Y.).—Goode and Bean (in part), Oceanic ichthyology, p. 290, pl. 74, figs. 263–263a, 1895 (specimens of at least three species included in this account; those from *Albatross* Sta. 2378 and 2402 included in account of *anatirostris* (p. 635); specimen from Sta. 2134 designated as holotype of *magnisquamis* (p. 633); other specimens are included below in account of *gobioides;* some of the listed specimens not now available for examination).

Bembrops gobioides Longley, Carnegie Inst. Washington Publ. 535, p. 237, 1941 (Tortugas, Fla.).

Description: D VI; 17–18. A 17–19. P 26–28. Sc 62–71. GR 4–5 + 14–16. Dorsal rays most predominantly 17, rather infrequently 18. Anal rays with the mode decidedly at 18, sometimes 17 or 19. Pectoral rays modally 27, varying 26–28. Gill rakers, including tubercles, on upper limb predominantly 5, sometimes 4; on lower limb modally 15, varying 14–16; total on both limbs modally 20, varying 18–21.

Measurements of four specimens 162–176 mm. in standard length, approximately 191–208 mm.: Caudal 18–19 (in two), pectoral 23.5–24.5, pelvic 15.2–16.7, depth 11.2–14.1, peduncle 4.9–5.6, head 33.5–37.0, maxillary 13.1–14.9, snout 10.5–11.9, eye 8.6–10.2. Ratio of eye in snout given in table 4.

Nearly all available specimens have almost all scales on body missing and normal color pattern not evident. They have a dark reticulate pattern made up of the prominent outlines of the scale pockets. Some specimens show two or three faint dusky smudges along lateral line. First dorsal usually black or dusky for its anterior upper and greater part, hyaline basally and posteriorly, often dark nearly all over; second dorsal moderately dusky margined with blackish and a basal blackish area at its anterior part; anal moderately dusky, rather narrowly margined with black, often dusky or black nearly all over; caudal dusky, usually with a rather wide black area at its distal end, and a dark area at its upper margin and in juxtaposition to the caudal peduncle, the latter probably representing a transformation of the juvenile caudal spot; pectoral usually more or less dusky all over and with a dark, transverse, curved band at its base; pelvic nearly pigmentless basally, dusky distally.

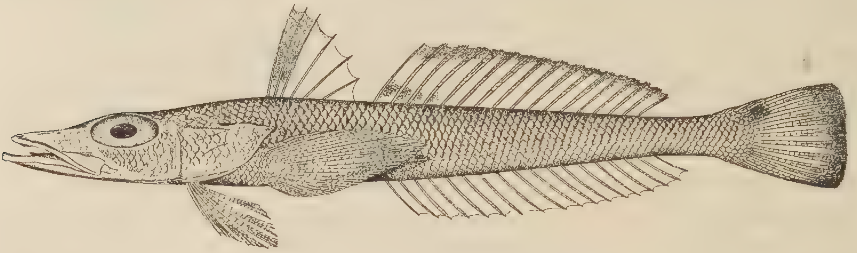

Figure 121.—*Bembrops gobioides*, from Goode and Bean, from a specimen (USNM 44233) taken off the Mississippi Delta. Caudal fin damaged in specimen figured; normally, caudal somewhat emarginate with the upper rays slightly longer than lower. Caudal spot disappears in large specimens.

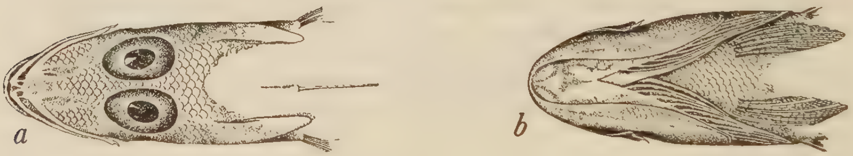

Figure 122.—*Bembrops gobioides*: *a*, dorsal aspect of head; *b*, ventral aspect of head; mandible more extensively scaled than shown in figure. (Both from Goode and Bean.)

Specimens examined: Tortugas, collected by Longley (USNM 92040). Collected by the *Oregon* and the *Albatross* in 65–280 fathoms off the following localities: Cape San Blas, Fla. (USNM 45744, 45975, 45973, 157727). Pensacola, Fla. (USNM 157726). Mississippi Delta (USNM 44233, 157728–30). Corpus Christi Pass, Tex. (USNM 157731–2). The preceding 12 lots comprise 50 specimens 81–220 mm. in standard length, approximately 95–260 mm. The foregoing account of the species is based chiefly on these specimens from southern Florida and the northern coast of the Gulf of Mexico. The single small specimen (26007) on which the species was originally based had been taken farther north as follows: *Fish Hawk* Sta. 871, lat. 40°02′54″ N., long. 70°23′40″ W., off Long Island, N. Y., 115 fathoms, Sept. 4, 1880. This holotype, about 43.5 mm. in standard length, the caudal damaged, is now in bad condition and altogether faded. The number of pectoral rays and scales are not definitely determinable. Other counts are as follows: D VI; 17. A 18. GR 5+15. Judged by these determinable counts it is apparently conspecific with the 50 southern specimens listed above; but it is of course necessary to examine a well preserved sample from the type locality to be certain of this identification.

Comparison: This species averages the highest fin ray and scale counts. It is nearest *anatirostris* and the differences between them are discussed under that species (p. 637).

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THE EFFECTS OF TEMPERATURE AND PREDATORS ON THE ABUNDANCE OF THE SOFT-SHELL CLAM, *MYA ARENARIA*, IN NEW ENGLAND

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ABSTRACT

Explanation of the recent decrease in production of the soft-shell clam in New England is the objective of the Fish and Wildlife Service Clam Investigations. Experimental clam farms failed unless protected from green crabs, *Carcinides maenas*. Laboratory experiments proved that *Carcinides* is a serious predator.

Clam abundance decreased 50 percent in 4 years in study areas even though fishing intensity was very low and reproduction was adequate. Population decrease occurred principally in places where green crabs had become abundant, and in size groups which are attacked by crabs. Clam population on commercial flats decreased from 1949 to 1954 and recent year classes are scarce or absent. Green crabs became abundant during this period.

Scientific records and interviews of fishermen indicate a northeastward extension of the range of the green crab since 1940 and great increase in abundance in Massachusetts, New Hampshire, and Maine. This extension was accompanied by decrease in clam production.

An increase in the abundance of green crab in the northern part of its present range is correlated with the current warm cycle. Winter temperatures are important to survival of green crabs since they and their eggs are reported to be killed by a combination of low temperature and low salinity. Warm winters allow more crabs to survive. Predation was accepted as the principal reason for the decrease in soft clams in Massachusetts and Maine. The future of the soft clam industry depends on the temperature cycle or on development of measures for controlling green crabs.

INTRODUCTION

Commercial production of the soft-shell clam in Massachusetts decreased from 8,598,100 pounds in 1940 to 625,000 in 1948. The output remained high in the State of Maine during this period but the industry and the Maine Department of Sea and Shore Fisheries became alarmed over the possibility that a similar decrease might occur in this State. The Fish and Wildlife Service was authorized by Congress in 1948 to determine the reasons for the decrease of soft-shell clams and to recommend measures for restoring production to a higher level.

Since 1948 Massachusetts clam production has remained at a low level. The slight increase during 1950 to 1952 (Fig. 1) was caused by marketing of clams from Boston Harbor after they had been cleansed to reduce coliform counts.

Maine's production decreased steadily from 8,969,000 pounds in 1948

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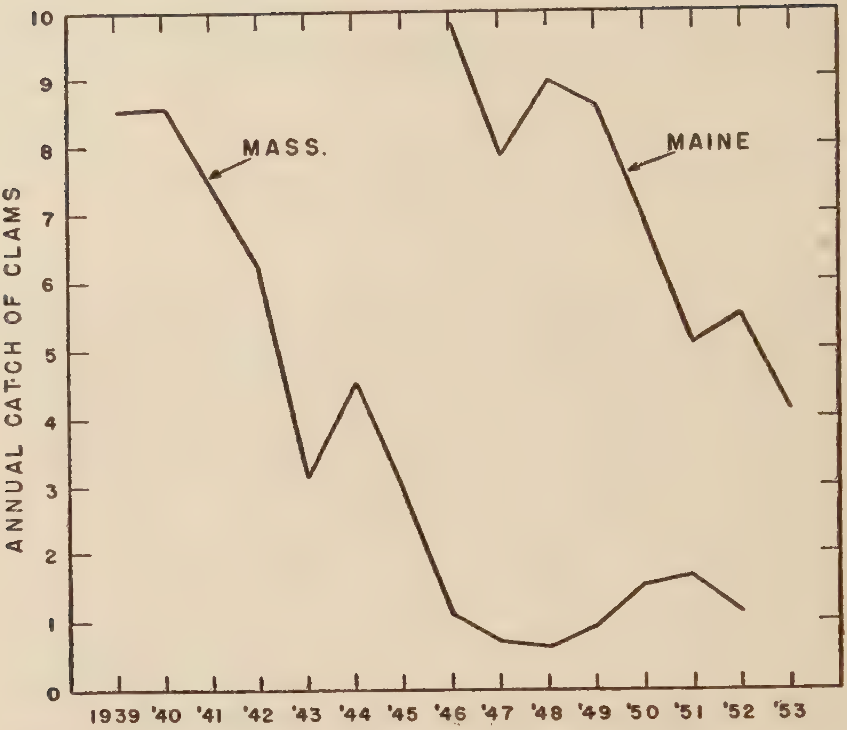

FIGURE 1.—Annual catch (millions of pounds of meats) of soft-shell clams in Massachusetts and Maine during the recent decline. Source: Fishery Statistics of the United States, (Anderson and Peterson 1953 and 1954)

to 4,148,000 pounds in 1953. This decline was alarmingly similar to that which occurred in Massachusetts about 8 years earlier.

Overfishing was generally believed to be the cause of the clam scarcity when our investigations began in 1948. Prices were high, market demand was heavy, and the fishery was intensive. If overfishing were truly the cause, two approaches were indicated: first, development of methods of farming clams similar to those used with oysters; and second, productivity studies to determine how many clams could be harvested each year without causing depletion.

EXPERIMENTAL CLAM FARMS

Clam farming was the first method which we tried for increasing production. We found an excellent source of small clams at Scarborough, Maine, and developed a hydraulic seed clam rake which would remove these clams from the sand so that they could be transplanted.

During 1950 and 1951 we planted seed clams in five places in Maine.

All of these farms failed except that in Sagadahoc Bay. Each failure could be directly traced to predation by the green crab, *Carcinides maenas*. The farms at Southport and Spurwink River lasted only 3 weeks. At Jonesport some clams survived for 2 or 3 months. At Wells most of the clams were eaten by crabs during the first 6 months.

The abundance of green crabs in the center of Sagadahoc Bay was very low during this period and the success of this farm could be attributed to their scarcity. Since that time the green crab abundance in Sagadahoc Bay has gradually increased so that we would not expect the same degree of success in clam plantings at the present time. The crab population at Wells was low at the time we planted the clams but increased immediately afterwards. Succeeding plantings by the Maine Department of Sea and Shore Fisheries 2 months later were consumed in a few weeks. Our plantings survived up to 6 months because the clams had a chance to become established and grow before the green crabs invaded this area.

Later farms were protected from predators and the clams survived and grew well. Some plantings were covered with 1-inch-mesh chicken wire laid directly on the flats. This protection excluded the green crabs, but was exceedingly expensive. Recently our biologists have developed a low chicken-wire fence (Smith, 1953) which excludes green crabs and which costs less per unit area than covering with screen. The clam farms demonstrated the importance of predators. Soft clam farming can only be recommended as a method of increasing production if predation by green crabs can be controlled.

Sagadahoc Bay Productivity Studies

In 1949 we chose Sagadahoc Bay on Georgetown Island, Maine, as a study area to determine the relationship between commercial fishing and abundance of clams and to develop methods for establishing an optimum fishing level. Each year since that time we have conducted a population census of the clams in this Bay. We have also obtained catch records from the commercial fishery. Fishing intensity has remained low during all of this period; in fact, during 1951 and 1952 the fishing effort was negligible since most of the diggers were employed at Bath Iron Works building destroyers. Since that time many diggers have returned to the flats but their production has remained low.

We feel that setting has been adequate each year. Early each spring we found a good population of clams—10 to 100 per square foot—from the spawning of the previous summer. By autumn practically all of these small clams had disappeared. In places where the green crabs have been excluded by fencing or screening, survival and growth have been excellent. We accordingly believe that green crabs are responsible for the disappearance of the young clams. In laboratory experiments medium-sized green crabs consumed up to 15 small *Mya* per crab per day. Therefore, a moderate population of crabs could consume an entire year class of small clams in a short time.

The population of clams over 25 millimeters long in Sagadahoc Bay has decreased from 40 million to 18 million during the period from 1949 to 1953 even though the commercial fishery has remained at a very low level. Most of this decrease has been in the illegal-sized clams, from 26 to 50 millimeters in length. The principal decrease occurred in areas A and B (Fig. 2) near the shore of Sagadahoc Bay. The population in area C, which is in the center of the Bay, has remained nearly constant.

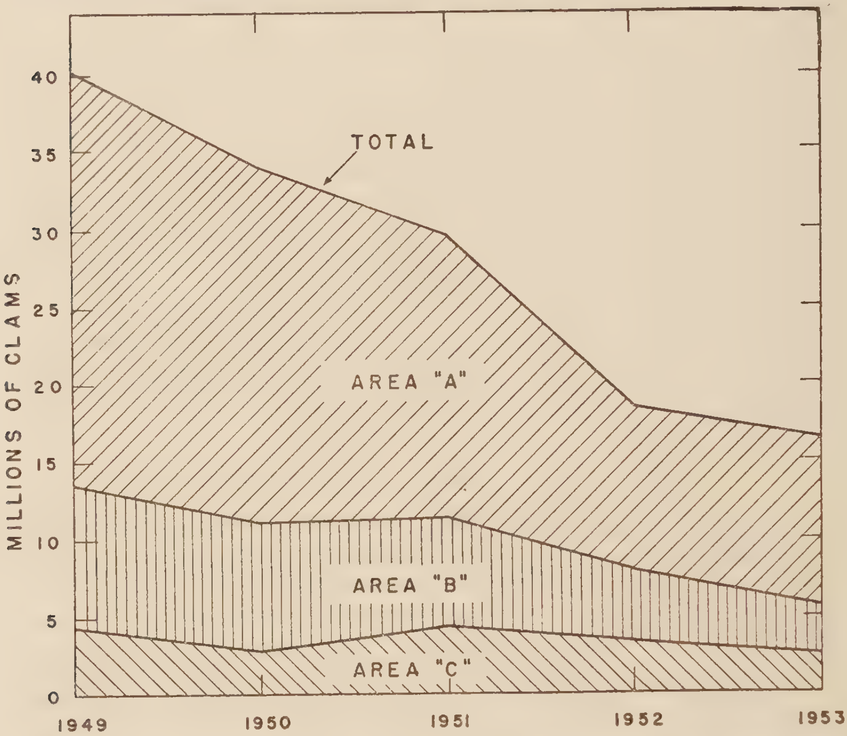

FIGURE 2.—Estimated population of clams over 25 millimeters long in different areas of Sagadahoc Bay, Maine, 1949–1953.

The crab population of Sagadahoc Bay has increased greatly since 1949, particularly near shore in areas A and B. Green crabs require a hiding place at low tide and, therefore, the areas around the edge of the Bay are more suitable than the broad sandy bottom in the center. We believe, therefore, that the decrease in abundance of small clams in areas A and B is correlated with the increase in the number of green crabs in those areas.

CLAM POPULATION SURVEYS

Biologists of Maine Department of Sea and Shore Fisheries sampled representative flats in eastern Maine to determine the size composition of clams and related species during 1949 to 1951. In the spring of 1954 State and Federal biologists resurveyed several of these flats with discouraging results as shown in Table 1.

Clam populations were lower in most areas surveyed in 1954 than they were at the first surveys in 1949 or 1950. Green crabs were present in 1954 on flats where they were not found in the original surveys. Clams from the 1950, 1951, and 1952 sets were extremely scarce or absent in many areas. When these areas were surveyed in the spring of 1954 some of the 1953 set were still present but these clams were so small that they may have been missed by green crabs. By next autumn these clams also may have been eaten.

The future of the clam fishery in eastern Maine appears to be very dark. Only in Holmes Bay and in part of Randall Point flats did we find a good size distribution of clams. In these broad flats the green crabs have few places to hide at low tide. Some crawl under the rockweed high on the beach during ebb tide and move out in search of food when the tide covers the flats. Other crabs move offshore with the ebb tide and return with the flood. Between these two bands is an area where predation is less severe. Therefore, green crab predation is serious only on small parts of the Randall Point and Holmes Bay flats.

Great Bar at Jonesport maintains a moderate clam population because of the gravel which gives the clams protection from their enemies. Even here the 1953 year class was extremely low and it is likely that many of this group were consumed by the hordes of small crabs.

GREEN CRAB ABUNDANCE

Predation by green crabs must have become more serious during recent years if this is the cause of the present scarcity of clams. Two possible factors which might have increased the importance of predation are 1) a northward extension of the range of green crabs and 2) an increase in their numbers.

Green crabs are temperate water crustaceans which apparently are moving northward in response to the current warming trend cycle (Fig. 3). Sidney I. Smith (1874 and 1879) reported that the green crab occurred only south of Cape Cod. By the early 1900's it was present in Casco Bay, Maine, as reported by Rathbun (1905). Rathbun (1930) gave the range as Thomaston, Maine, to New Jersey. In 1930, two lots of green crabs were collected at Brooklin, Maine. Scattergood (1952) reported green crabs at Winter Harbor, Maine, in 1939, but none northeastward of this location as late as 1942. By 1950, green crabs were seen at Great Bar, Jonesport, Maine, by biologists of the Maine Department of Sea and Shore Fisheries.[1] U. S. Fish and Wildlife Service biologists found crabs at Cummings Beach at Jonesport, Maine, in 1951 when planting an experimental clam farm. Scattergood found one specimen at Carrying Place Cove, Lubec, in June 1951, establishing a northeastern record. Shortly thereafter

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[1] Information from Louis Taxiarchis of the Maine Department of Sea and Shore Fisheries, Augusta, Maine.

TABLE 1.—*Summary of clam population surveys in Maine conducted by the Maine Department of Sea and Shore Fisheries and the U. S. Fish and Wildlife Service*

Area	Date of survey	Clams per square foot		Size distribution	Green crabs	Remarks
		Over 1 year old	1 year old			
Calton Point Jonesboro, Maine	1949	10.5	(see remarks)	Good — each year class present	None	Population including spat and clams up to 1¾ inches was 75 per square foot
	1954	2.2	7.5	1952 set — none 1951 do. — do. 1950 do. — scarce 1949 do. — common	Very abundant	
Deep Hole Point Jonesboro, Maine	1949	10.5	(see remarks)	Good — each year class present	None	Many small clams near high tide line
	1954	4.0	1.9	1952 set — scarce 1951 do. — do. 1950 do. — common 1949 do. — abundant	Abundant	
Randall Point Machiasport, Maine	1949	5.7	?	Good — each year class present	None	
	1954	4.1	14.9	1952 set — none 1951 do. — scarce 1950 do. — do.	Abundant (see remarks)	Excluding middle of flats where crab predation is less severe
Holmes Bay Machiasport, Maine	1949	6.8	Scarce	Most over 2 inches but each year class present	None	
	1954	4.2	6.3	1952 set — none 1951 do. — scarce 1950 do. — common 1949 do. — abundant	Common	Predation moderate; area unsuitable for large crab population

Area	Date of survey	Clams per square foot		Size distribution	Green crabs	Remarks
		Over 1 year old	1 year old			
Great Bar Jonesport, Maine	1950	5.9	?	Good — each year class present	Abundant (see remarks)	All crabs less than ½ inch in width
	1953	7.1	2.1 (see remarks)	Good — each year class present	Abundant	Spat count includes some 1953 set. Crab predation low because of gravel
	1954	8.6	None	Mostly larger clams but each year class present	Very abundant (see remarks)	Many very large green crabs, but predation low because of gravel
Sam's Cove Bremen, Maine	1949	15.2 to 41.6	Extremely abundant	Excelent population of each year class	None	Population so high that experiment set up to determine if thinning would improve growth
	1954	None	2.3	No clams over 10 millimeters present except in thatch grass	Extremely abundant	Good size distribution of clams in thatch grass and gravel where they are safe from crabs
Cummings Beach Jonesport, Maine	1941	....	....	....	None	Experimental clam farms successful
	1951	?	?	Each year class present but most of legal size removed by diggers	Common	Experimental clam farm established in April; destroyed by crabs during summer. Digging prohibited
	1954	2.3	5.0	1952 set — none 1951 do. — do. 1950 do. — scarce 1949 do. — common	Extremely abundant	Digging permitted, but few small clams present. Crabs nearly as abundant as in Massachusetts

in July and September 1951 Canadian biologists found green crabs at Oven Head, Digdeguash at Passamaquoddy Bay. This locality was the northeastern end of the range as reported by Scattergood (1952). During 1953, Canadian biologists observed green crabs on the north shore of the Bay of Fundy as far east as Point Lepreau, on the south shore at Pereau River in Minas Basin, and at Sandy Cove in St. Mary Bay, Nova Scotia. The northeastern range was extended farther in August 1954 by the discovery of one specimen at Wedgeport, Nova Scotia.[2]

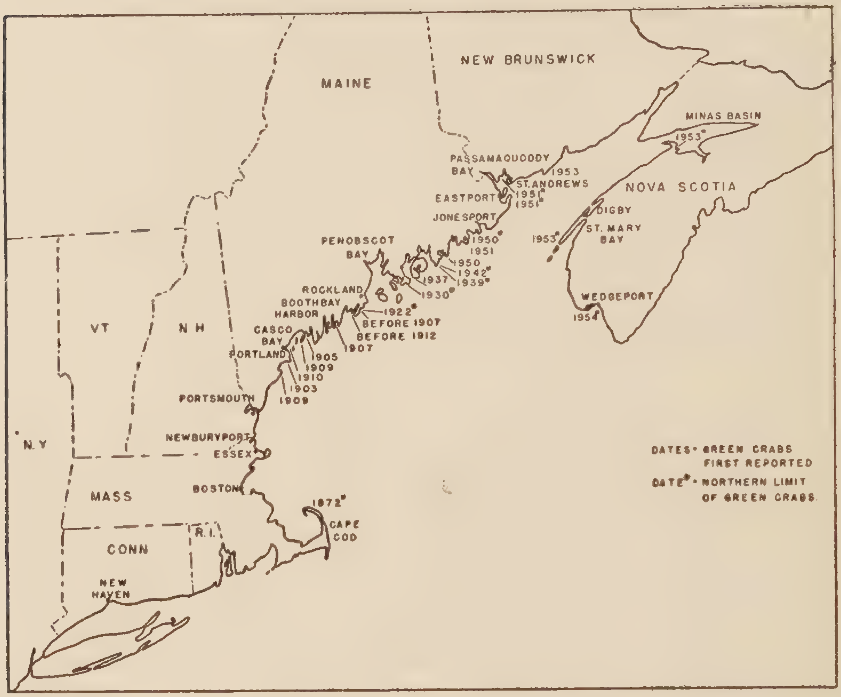
MAINE
NEW BRUNSWICK
MINAS BASIN
1953*
PASSAMAQUODDY BAY
1953
ST. ANDREWS
1951*
1951*
EASTPORT
JONESPORT
NOVA SCOTIA
DIGBY
ST. MARY BAY
1953*
PENOBSCOT BAY
1950*
1951
1950
1942*
1939*
1937
1930*
ROCKLAND
BOOTHBAY HARBOR
1922*
BEFORE 1907
BEFORE 1912
1907
CASCO BAY
PORTLAND
1905
1909
1910
1903
1909
WEDGEPORT
1954
VT
N H
N. Y
PORTSMOUTH
NEWBURYPORT
ESSEX
BOSTON
MASS
1872*
CAPE COD
R. I.
CONN
NEW HAVEN
DATES • GREEN CRABS FIRST REPORTED
DATE* • NORTHERN LIMIT OF GREEN CRABS.

FIGURE 3.—Map of New England showing dates when green crab, *Carcinides maenas*, was first reported. Dates marked with asterisk indicate northern limit of green crabs at that time.

Scientific observations listed above are corroborated by statements from diggers and lobster fishermen along the Maine Coast. During January and February 1952 wardens of the Maine Department of Sea and Shore Fisheries questioned over 100 clam diggers and lobster fishermen. Each man was asked when he had first seen green crabs, or had first caught them in his traps. On the basis of their replies (Table 2), Maine can be divided into two areas: (1) West of Penobscot Bay where the green crabs have been present for as long as living man can remember, *i.e.*, about 1900 to 1915; (2) East of Penobscot Bay where green crabs have been seen only during the last 2 to 10 years, except for one questionable observation in 1919. Some areas existed at the time of this survey where fishermen had not yet found green crabs.

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[2] Information from J. S. MacPhail of the Fisheries Research Board of Canada, St. Andrews, New Brunswick.

TABLE 2.—*Summary of replies to Maine Department of Sea and Shore Fisheries questionnaire indicating when green crabs were first seen in Maine*

Year	Entire State	West of Penobscot Bay	East of Penobscot Bay	Year	Entire State	West of Penobscot Bay	East of Penobscot Bay
1951........	5	..	5	1919........	1	..	1
1950........	9	..	9	1915........	2	2	..
1949........	7	1	6	1914........	1	1	..
1948........	6	1	5	1913........	1	1	..
1947........	3	3	..	1912........	3	3	..
1946........	2	1	1	1911........	1	1	..
1945........	3	2	1	1910........	1	1	..
1943........	1	1	..	1909........	1	1	..
1942........	4	1	3	1907........	3	3	..
1938........	3	1	2	1903........	1	1	..
1933........	1	1	..	1900........	1	1	..
1932........	2	2	..				
1927........	2	2	..	Total replies.	64	31	33

Question No. 2 of the Sea and Shore Fisheries questionnaire circulated by the wardens in 1952 asked, "When in the past were green crabs plentiful in Maine?" The replies (Table 3) indicate no well-defined break at Penobscot Bay as was found for dates when green crabs were first reported by the fishermen. In all areas most reports indicated crabs were more plentiful in 1951 than at any earlier time. Division of replies into areas East and West of Penobscot Bay suggests that crabs have been plentiful

TABLE 3.—*Summary of replies to Maine Department of Sea and Shore Fisheries questionnaire indicating when green crabs were most plentiful in Maine*

Year	Entire State	West of Penobscot Bay	East of Penobscot Bay	Year	Entire State	West of Penobscot Bay	East of Penobscot Bay
1951........	45	22	23	1938........	2	2	..
1950........	20	9	11	1937........	2	2	..
1949........	13	9	4	1936........	2	2	..
1948........	9	7	2	1935........	2	2	..
1947........	6	6	..	1934........	2	2	..
1946........	6	6	..	1932........	2	2	..
1945........	5	5	..	1931........	1	1	..
1944........	4	4	..	1930........	1	1	..
1943........	4	4	..	1929........	1	1	..
1942........	4	3	1	1928........	1	1	..
1941........	2	2	..	1927........	1	1	..
1940........	2	2	..	1926........	1	1	..
1939........	2	2	..				
				Total replies.	140	99	41

in places in the western part of the State since 1934, but not generally so until 1949 to 1951. East of Penobscot Bay crabs have been plentiful only since 1948, except for one record of 1942 at Tremont. These replies agree with the answers to Question No. 1 in indicating that green crabs have been present for many years west of Penobscot Bay and have merely increased in abundance since about 1948. East of Penobscot Bay the absence of early observations of great abundance of green crabs may indicate that the crabs have only recently spread into that area.

The best record of changes in green crab abundance that we have found are those of Franklyn Goucher who, for a number of years, was Clam Commissioner for the Town of Essex, Massachusetts.[3] Mr. Goucher described the abundance of green crabs and clams at Essex, Massachusetts, for the period from about 1924 to 1951. He stated that he first saw green crabs there in 1926 and that they became more numerous each year into the early 1930's. Clamming became poorer during this period, and by 1931 no diggers remained. The coldest winter on record, 1933–34, killed the crabs according to Goucher, and from that time until 1944 few were seen. Clamming was good during this period; in fact, records show the peak of production of 8.5 million pounds in Massachusetts was reached in 1940.

Goucher stated that the abundance of crabs gradually increased from 1944 to 1947 until the diggers saw one or more every tide instead of one or two per year as in the period from 1933 to 1934. In the autumn of 1948, Goucher saw green crab pits over the entire flats as he had in the late 1920's, and found 350 crabs in one hole in a thatch bank. Clam production had dropped to less than a million pounds a year by this time. By 1949 lobster fishermen were again complaining that the crabs were filling their pots and eating the bait. Goucher said that 1950 and 1951 brought even more crabs and fewer clams, just like 1930 and 1931.

TEMPERATURE TRENDS

Clayton (1944, 1944a, and 1947) listed monthly mean air temperatures at New Haven, Connecticut, since 1778. Means for the coldest month of each winter smoothed by a 21-year moving average, are shown as a solid line in Figure 4. The dotted line from 1945 to 1954 indicates a moving average based on a decreasing number of years from 20 to 11. This section of the graph, therefore, is not strictly comparable with the preceding years.

The coldest period at New Haven was during the years from 1820 to 1840 when winter temperatures averaged between 23° and 24° F. In 1850 to 1860 winter temperatures averaged 24° to 25°. By 1900, temperatures for the coldest month of the winter averaged 25° to 26° F. In the 1920's, winter temperatures were averaging close to 27°, and in 1944, which is the last year in which it was possible to compute a 21-year moving average, the winter temperature averaged 27.8°. Since that time, the temperature has continued to climb and the temperature average for 1954, based on 11 years' records, was 29.0° F. The highest actual temperature recorded for the coldest month of a winter was during 1953 when January averaged 34.2°. Since the 1820–1840 period, minimum winter temperatures as indicated by 21-year moving averages, have risen about 4° F.

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[3] Goucher, Franklyn E. 1951. Commentary of a clam digger. Unpublished manuscript on file at U. S. Fish and Wildlife Service, Fishery Laboratory, Boothbay Harbor, Maine.

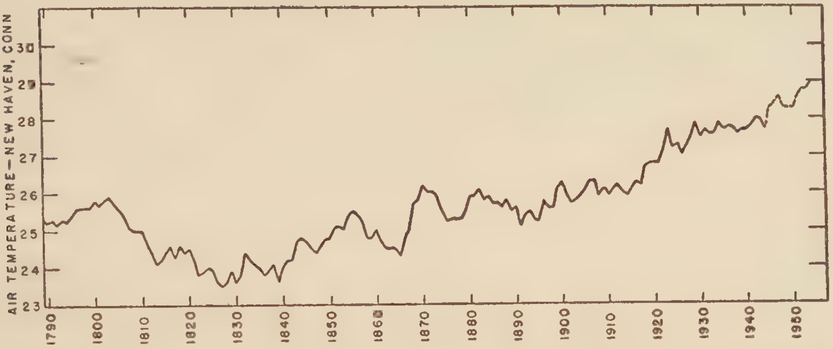

FIGURE 4.—Mean air temperatures for coldest month of the winter at New Haven, Connecticut, smoothed by a 21-year moving average from 1789 to 1944 (solid line) and by 20 to 10 year averages from 1945 to 1954 (dotted line).

Mean monthly surface water temperatures are available since: 1906 for Boothbay Harbor, Maine; 1921 for St. Andrews, New Brunswick; 1922 for Boston, Massachusetts; and 1930 for Eastport, Maine. Temperatures at these stations agree closely. Averages for the coldest month of the winter for Boothbay Harbor, Maine, are plotted in Figure 5. The coefficient of correlation for the unsmoothed air temperatures at New Haven, Connecticut, and water temperatures at Boothbay Harbor for coldest month of the winter is 0.701. This highly significant correlation permits extrapolation of water temperatures to previous years for which only air temperatures were recorded. Therefore, it is safe to conclude that water temperatures have risen along with the air temperatures indicated in Figure 4, although it is not possible to identify short-term cycles of water temperature from the air-temperature records.

TEMPERATURE TRENDS AND ABUNDANCE OF GREEN CRABS

There is good evidence that *Carcinides* is a temperate-water crab. Franklyn Goucher, the Clam Commissioner of Essex, Massachusetts, reported a mass mortality of green crabs during the cold winter of 1933–34. Broekhuysen (1937) stated that low temperatures and low salinities will kill green crabs. Another possibility is that low temperatures destroy the eggs which the females carry through the winter attached to their pleopods.

The northeastward spread of *Carcinides* may have been permitted by the warming trend which began about 1840 (Fig. 4). Smith's (1879) observations in 1871–72 that green crabs occurred only south of Cape Cod were made at the beginning of a short-term warming cycle when winter temperatures were low. Belding (1909 and 1931) did not even list *Carcinides* as a clam predator in Massachusetts. Kingsley (1901) found no green crabs in Casco Bay, Maine. Shortly thereafter Rathbun (1905) and Morse (1909) observed green crabs in the same general area. During the late 1930's when green crabs first appeared East of Penobscot Bay, the minimum monthly water temperature at Boothbay Harbor was 32.5° F. In the late 1940's and early 1950's when the crabs spread to eastern Maine, New Brunswick and Nova Scotia, the average minimum temperature was the highest on record, 36° to 38°.

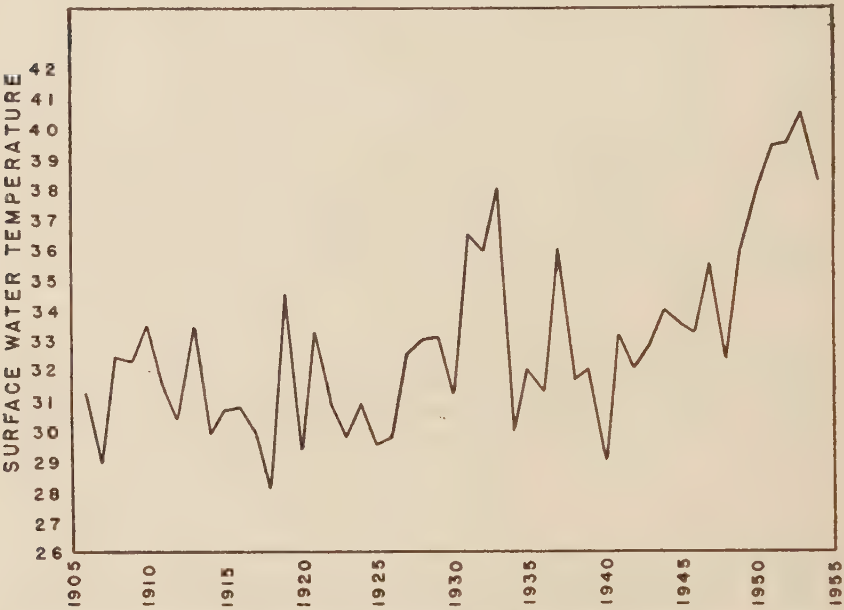

FIGURE 5.—Mean surface water temperature (°F.) for coldest month of the winter at Boothbay Harbor, Maine.

Fluctuations in the abundance of green crabs may have been caused by short-term temperature cycles (Fig. 5). The 1923–1933 warming trend coincides with the increase in green crabs in Essex, Massachusetts, as reported by Goucher. Likewise the cold winter of 1933–34 was accompanied by a great decrease in crabs.

There are some indications of a similar trend in the abundance of green crabs in southern Maine during the 1923–1934 cycle but not in northeast Maine. Four fishermen reported green crabs to be scarce in Casco Bay after the cold winter of 1933–34. They did not, however, consider the crabs "abundant" before 1934. Possibly temperatures in southern Maine were too low to permit a great increase in crabs during this cycle, and the partial destruction of the small population went unnoticed by most of the fishermen. Apparently green crabs had not become established east of Penobscot Bay at this time.

The present warm-water cycle has been accompanied by an increase in green crabs in Massachusetts, New Hampshire, Maine, New Brunswick and Nova Scotia. This warming trend following a low of 29.1° F. in February 1940 at Boothbay Harbor has established a record high of 40.6° F. in January 1953. All of the winters from 1950 through 1954 exceeded the previous record for the mildest winter established in 1932–33. The last five mild winters doubtless permitted the spread of green crabs to eastern Maine, New Brunswick and Nova Scotia.

OUTLOOK FOR THE CLAM INDUSTRY

The discussion of the decrease in clam production, the coincident increase in green crab abundance, and increase in temperature is undoubtedly an oversimplification of the problem. The actual relationships among these factors are far more complex, and it will require much more information to clarify them. Nevertheless, the correlation between green crab abundance and clam scarcity is good enough to justify acceptance of predation as the principal reason for the decrease of soft clams in Massachusetts and Maine.

We are asked repeatedly about the future of Maine's clam industry. At the present time the outlook is very dark. Production may continue to drop, as it did in Massachusetts, if the weather remains mild. On the other hand, one or two cold winters might reduce the green crab population and allow the stocks of clams to recover.

We are continuing research on methods of controlling crabs including fencing, electrical barriers, poisons, and biological control. Further research is necessary on the severity of winter needed to kill the crabs.

We also want to know what factors control the green crab population south of Cape Cod. Fishermen say that green crabs have not increased in Rhode Island during the past 10 years. In fact, some state that the crabs have become scarce. Possibly the enemies of green crabs in those areas also may extend their range and stabilize the crab population north of Cape Cod at a level which will permit a clam fishery of moderate intensity.

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I am indebted to several individuals and agencies who assisted in this study. Fish and Wildlife Service biologists Osgood R Smith, John P. Baptist, Warren S. Landers, Walter R. Welch, and Harlan S. Spear provided extensive data from field and laboratory studies concerning clams and crabs. Biologists Robert L. Dow, Dana Wallace, and Louis Taxiarchis of the Maine Department of Sea and Shore Fisheries provided information concerning clam surveys, questionnaires, and observations of their agency as well as cooperating in field studies. Fisheries Research Board of Canada biologist J. S. MacPhail and oceanographers Louis Lauzier and H. B.

Hachey provided information on distribution of green crabs in Canada and on water temperatures at St. Andrews, New Brunswick.

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SURVIVAL OF SOFT-SHELL CLAMS, *Mya Arenaria*, BURIED AT VARIOUS DEPTHS

by

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ABSTRACT

Commercial diggers leave sub-legal clams buried at 1 inch to 9 inch depths in positions ranging from upright to inverted. One or both valves of some of these clams may be broken by the digging operation. Survival of these clams, which must be known to evaluate the effect of the fishery have been determined in five experiments:

1. Clams with broken shells have less than one chance in a hundred of surviving.
2. The deeper clams are buried, the poorer are their chance of survival.
3. Survival of clams buried in upright and horizontal positions was significantly greater than survival in an inverted position. The difference between survival in upright and horizontal positions was not statistically significant.
4. Survival was better in silty-sand than in sand and poorest in silt.
5. Average survival in winter was greater than in summer.
6. Survival was directly proportional to the size of the clams.
7. Results of these experiments suggest the possibility of increasing production by limiting the frequency of digging and improving digging methods.

The commercial fishery affects a clam population in two ways: First, it removes a certain amount of clams which can be determined from diggers' and dealers' records; Second, many clams are broken and left behind by the diggers or are buried too deep to survive. These clams must be added to the catch to obtain the total removal by the fishery. The experiments reported here were conducted by the U. S. Fish and Wildlife Service and the Maine Department of Sea and Shore Fisheries to provide information on the survival of sub-legal clams left by commercial digging operations.

The author wishes to acknowledge the valuable assistance of Walter R. Welch and Harlan S. Spear, Fishery Research Biologists, and William J. Brown, Fishery Aid, U. S. Fish and Wildlife Service, and Dana Wallace, Maine Department of Sea and Shore Fisheries in conducting the extensive field work necessary to complete this experiment.

Soft-shell clams live buried in the intertidal zone to a depth of two or three times their shell length. A 2-inch clam, the minimum legal size in most states, would be covered by 4 to 6 inches of sediment. In commercial digging operations the overlying sediment is removed with a tined fork or " clam hoe " and the legal-sized clams are picked out.

In one digging method, the top 4- to 6-inch layer containing the clams is removed in large chunks, which are turned upside down. The legal clams are then taken from the bottom of the chunks. This method leaves all the clams inverted. The smallest clams which were in the top 2 inches are buried several inches deep, whereas the larger clams are left close to the surface.

In the second digging method, the top 2- or 3-inch layer is removed and thrown backwards between the digger's legs and lands on top of the pile of previously dug sediment. The smaller clams which are in this top layer are deposited fairly close to the surface in various positions. The next 3- or 4-inch layer, which contains the larger clams, is turned over in large chunks, and the legal clams are removed from the bottom. This causes most of the clams just below legal size to be left inverted under several inches of loose sediment.

The question to be answered is, " What percentage of clams buried at different depths in upright, horizontal, or inverted position will survive in various sediment types and at various times of the year? "

METHODS

We conducted experiments in three coves at Georgetown Island, Maine, during the summer to compare survival of clams buried in sand, silty-sand and silt. The experiment in silty-sand was repeated during the following winter to compare the effect of seasons on survival.

In each cove we selected experimental areas of approximately the same tidal level and buried clams of three size groups in three positions and at three depths. Two weeks later we exhumed the clams and determined how many had survived under these conditions.

Each experiment was conducted in accordance with the following procedure:

1. Plots 4 feet apart were marked with stakes and numbered at random.
2. A hole at least 10 inches deep and 2 feet in diameter was dug at each plot to remove all native clams.
3. Clam-free sediment from below the 10-inch depth was taken from trenches adjacent to the experimental areas and placed in each hole until the desired level was attained. In the first two experiments clams were buried 1, 5, and 9 inches deep. In the last three experiments the depths of burial were 1, 3, and 5 inches.

4. The clams were divided into three size groups: 9-20 mm. (⅜ to ¾ inches); 21-35 mm. (¾ to 1⅜ inches); and 36-50 mm. (1⅜ to 2 inches). This nearly covered the size range of sub-legal clams, since the minimum legal length in most states is 2 inches.
5. Clams were planted in upright, horizontal, and inverted positions. " Upright " is the normal position in which clams occur, that is, with valves vertical and siphons extending toward the surface. " Horizontal " clams were placed on their sides with valves parallel to the surface of the sediment. " Inverted " clams were buried with their valves vertical with their siphons pointing downward.
6. Fifty clams of each size group were buried at each depth and in each of the three positions. Large clams in upright and inverted positions were carefully inserted in holes made in the soil with a finger or a pointed stick. This enabled us to place the clams in position with their umbones at the desired level without injury. Medium and small clams in upright and inverted positions and all clams in horizontal positions did not require this precaution since the sediment was soft enough to prevent injury to these clams.
7. After the clams had been placed in position, the holes were filled with clam-free sediment from the trenches adjacent to the experimental area.
8. Two weeks later the clams were exhumed, and the numbers alive and dead were recorded.

Table I shows a summary of the five experiments. Figure 1 shows a typical plot arrangement. Statistical analyses of significance of differences between percentages of survival were made by the chi square test, results of which are on file at the Department of Sea and Shore Fisheries, Augusta, Maine.

Table 1. — Summary of experiments 1 to 5

Experiment	Location	Soil type	Season	Depths in inches	Size of clams in mm.	Position	Condition
1	Center of Sagadahoc Bay	Sand	Summer	1, 5, 9	9-20 36-50	upr hor inv	broken and unbroken
2	Center of Sagadahoc Bay	Sand	Summer	1, 5, 9	9-20 21-35	upr hor inv	broken and unbroken
3	Bedroom Cove	Silty-sand	Summer	1, 3, 5	9-20 21-35 36-50	upr hor inv	unbroken
4	Birch Island Cove	Silt	Summer	1, 3, 5	9-20 21-35 36-50	upr hor inv	unbroken
5	Bedroom Cove	Silty-sand	Winter	1, 3, 5	9-20 21-35 36-50	upr hor inv	unbroken

Shore

Plot No. **12** Depth 3″ Size 9-20 mm Pos. inverted	**24** 5″ 21-35 mm inv	**22** 5″	**7** 1″	Plot No. **16** Depth 3″ Size 36-50 mm Pos. upright
15 3″ 21-35 mm inv	**5** 1″ 21-35 mm hor	**8** 1″ 36-50 mm hor	**17** 3″ 36-50 mm hor	**18** 3″ 36-50 mm inv
19 5″ 9-20 mm upr	**25** 5″ 36-50 mm upr	**13** 3″ 21-35 mm upr	**6** 1″ 21-35 mm inv	**29** Blank
14 3″ 21-35 mm hor	**4** 1″ 21-35 mm upr	**11** 3″ 9-20 mm hor	**10** 3″ 9-20 mm upr	**26** 5″ 36-50 mm hor
28 Blank	**9** 1″ 36-50 mm inv	**3** 1″ 9-20 mm inv	**27** 5″ 36-50 mm inv	**30** Blank
1 1″ 9-20 mm upr	**21** 5″ 9-20 mm inv	**2** 1″ 9-20 mm hor	**23** 5″ 21-35 mm hor	Plot No. **20** Depth 5″ Size 9-20 mm Pos. horizontal

Sea

Fig. 1 — Typical Plot Arrangement — Experiment 5, Bedroom Cove, February 25-March 11, 1953. All plot locations chosen from table of random numbers.

EXPERIMENTS 1 AND 2

Experiment 1.

This experiment was set up in the sand of the center of Sagadahoc Bay, Georgetown Island, Maine, on June 25, 1952, using 9-20 and 36-50 mm. clams. Clams from 16 of the plots were exhumed after 16 days and from the remaining 14 plots 3 days later.

Mortality of those clams whose shells were broken before planting was very high. We recovered 360 of the 700 broken clams which were planted, and 350 of these were dead. Of the 10 live clams, 8 had had only the edge of one valve chipped and were not seriously damaged; the other 2 were in the 36-50 mm. group and had had one valve actually broken. Survival, disregarding the 8 slightly damaged clams, was 2 out of 352 or 0.57 per cent. The results of this experiment, corroborated by experiment 2, show a broken clam rarely survives.

Experiment 2.

This experiment was started July 3, 1952 as a continuation of experiment 1, and the clams were exhumed 14 days later. Clams in the intermediate size group, 21-35 mm., were planted in all three positions at 1, 5, and 9 inches, and 9-20 mm. clams were buried inverted at 1- and 5-inch depths.

Survival of broken clams was low as indicated previously by experiment 1. We recovered 324 of the 447 broken clams planted, and 309 of these were dead. Of 15 live clams, 11 had only slightly chipped shells. Considering only the live clams recovered which had one valve actually broken, the survival was 4 out of 313 or 1.28 per cent. The combined survival of broken clams of all sizes in experiments 1 and 2 was 0.90 per cent. Therefore, in succeeding experiments we planted only undamaged clams.

Survival of unbroken clams varied inversely with the depth of burial as shown by figure 2 and table 2.

Table 2. — Percentage survival of unbroken clams buried in sand at various depths regardless of position — experiments 1 and 2.

Size group	Percentage surviving at depth of		
	1 inch	5 inches	9 inches
9-20 mm.	92.3	15.2	0.0
21-35 mm.	87.5	21.6	1.4
36-50 mm.	77.7	33.6	6.9

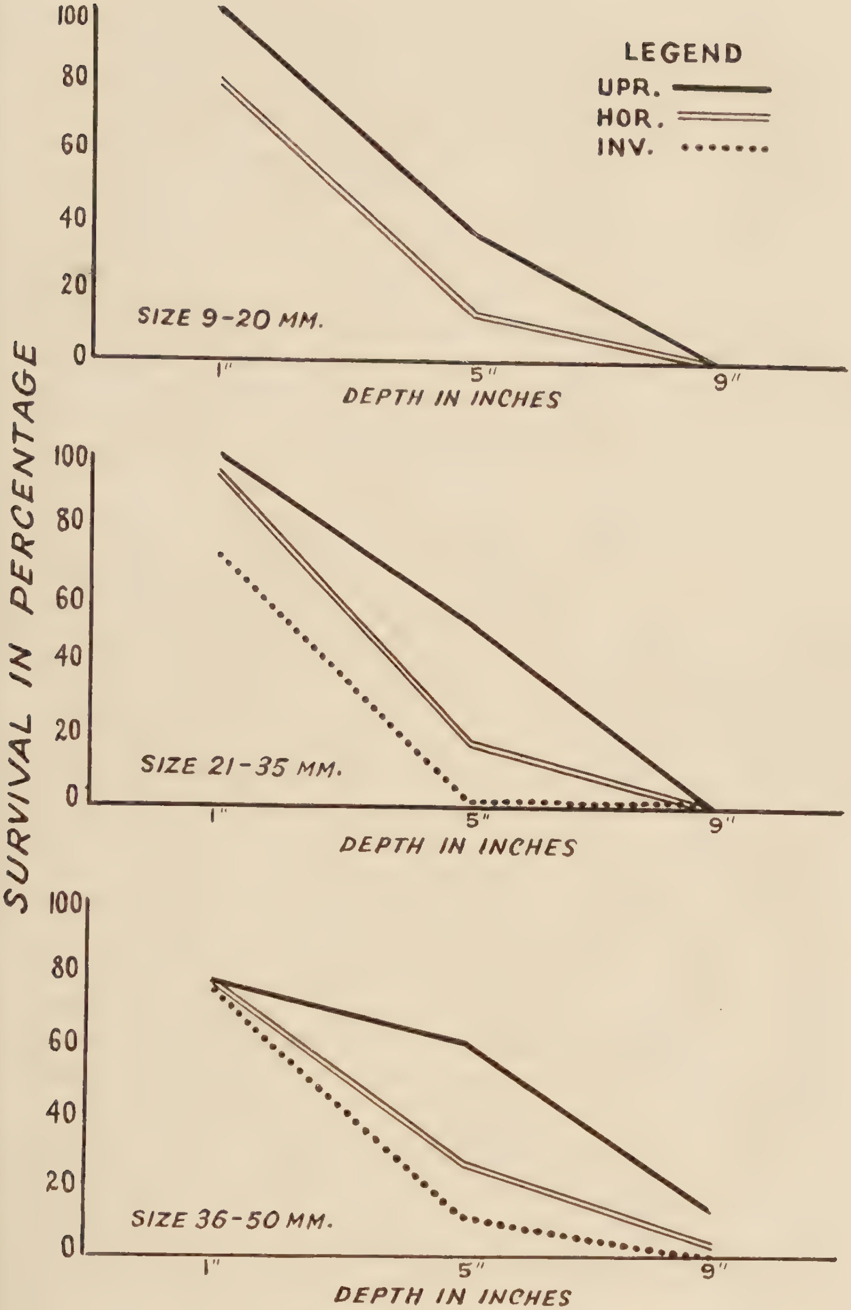

FIGURE 2. -- PERCENTAGE SURVIVAL OF UNBROKEN CLAMS IN SAND IN SUMMER - EXPERIMENTS 1 AND 2

In experiments 1 and 2, at a depth of 9 inches a significantly greater number of large clams than of medium or small clams survived but so few of any size survived at this depth that succeeding experiments included plantings at depths of 1, 3 and 5 inches only. At both 5- and 9-inch depths, survival of medium and large clams varied directly with size, but differences between small and medium clams were not statistically significant. At a 1-inch depth there were no statistically significant differences among the survival rates of various sizes.

At a depth of 5 inches, survival was better for clams planted upright than for those planted horizontal, and survival for horizontal clams was better than for those planted in an inverted position (figure 2). Differences in percentage survival were statistically significant for medium and large clams. Survival rates for the small clams appeared from figure 2 to follow the same relation, but too few clams were recovered to make the differences statistically significant.

At a depth of 1 inch, position of planting seemed to influence survival of the 36-50 mm. clams only slightly. Apparently at this depth the large clams were able to orient themselves readily regardless of their planted position. The 21-35 mm. group (figure 2) showed the same relation between survival and planted position as observed at the 5-inch depth. The 9-20 mm. group appeared from figure 2 to have better survival in upright than in horizontal position, but too few clams were recovered to demonstrate statistical significance. Table A-1 and A-2 in appendix A present detailed records of these two experiments.

Experiment 3

The third experiment was set up in the firm silty-sand of Bedroom Cove on the west side of Sagadahoc Bay on July 29, 1952, and concluded August 12, 1952. Only unbroken clams were used in this planting, and these were buried 1, 3 and 5 inches deep in upright, horizontal, and inverted positions. Table 3 shows survival of clams of each size regardless of position. Survival percentages for each size group and position appear in table A-3 in appendix A and in figure 3.

Survival of all size groups in all positions was good at a depth of 1 inch. Differences in survival rates were not statistically significant.

The large clams survived significantly better than small clams at 3-inch and 5-inch depths as shown in table 3.

Table 3.— Percentage survival of clams buried in silty-sand at various depths regardless of position — experiment 3.

Size group	Percentage survival at depth of		
	1 inch	3 inches	5 inches
9-20 mm.	95.3	58.9	17.7
21-35 mm.	94.0	78.7	40.3
36-50 mm.	93.7	91.2	55.6

In the 36-50 mm. group, at the 5-inch depth survival was better for upright clams than for horizontal and better for horizontal than for inverted. At the 3-inch depth there was no significant difference between survival in upright and horizontal positions but survival in both these positions was better than that of the inverted clams (figure 3).

In the 21-35 mm. group, at the 5-inch depth the difference in survival among the three positions was not significant. At the 3-inch depth survival was better for upright clams than for horizontal and significantly better for horizontal than for inverted.

In the 9-20 mm. group, survival in the various positions was erratic. At the 5-inch depth, horizontal clams had a 28 per cent survival, whereas only 19 per cent of the inverted and none of the upright clams survived. At the 3-inch depth, both upright and inverted clams had 59 per cent survival, whereas the horizontal clams had only 6.7 per cent. Variations in composition or compaction in this silty-sand area may have caused these variations in results. A chunk of firmly packed sediment placed on top of these small clams could suffocate them. Since the results for the 9-20 mm. clams at 3-inch depth were considered atypical, they were omitted from calculations. Detailed records of experiment 3 are given in table A-3 in appendix A.

Experiment 4

The fourth experiment duplicated experiment 3, except that the sediment was silt instead of silty-sand. The clams were planted August 14 and 15, 1952, in Birch Island Cove, Georgetown Island, Maine, and were exhumed August 28, 1952. Survival percentages in relation to planted position are shown in table A-4 in appendix A and in figure 4.

Survival of the 9-20 mm. group was poor in all positions at a 1-inch depth (figure 4); however, this trend may have been exaggerated by the poor recovery of planted clams (28 per cent). Pitting of the flats in the experiment area indicated digging activity of the green crab, **Carcinides maenas**, which

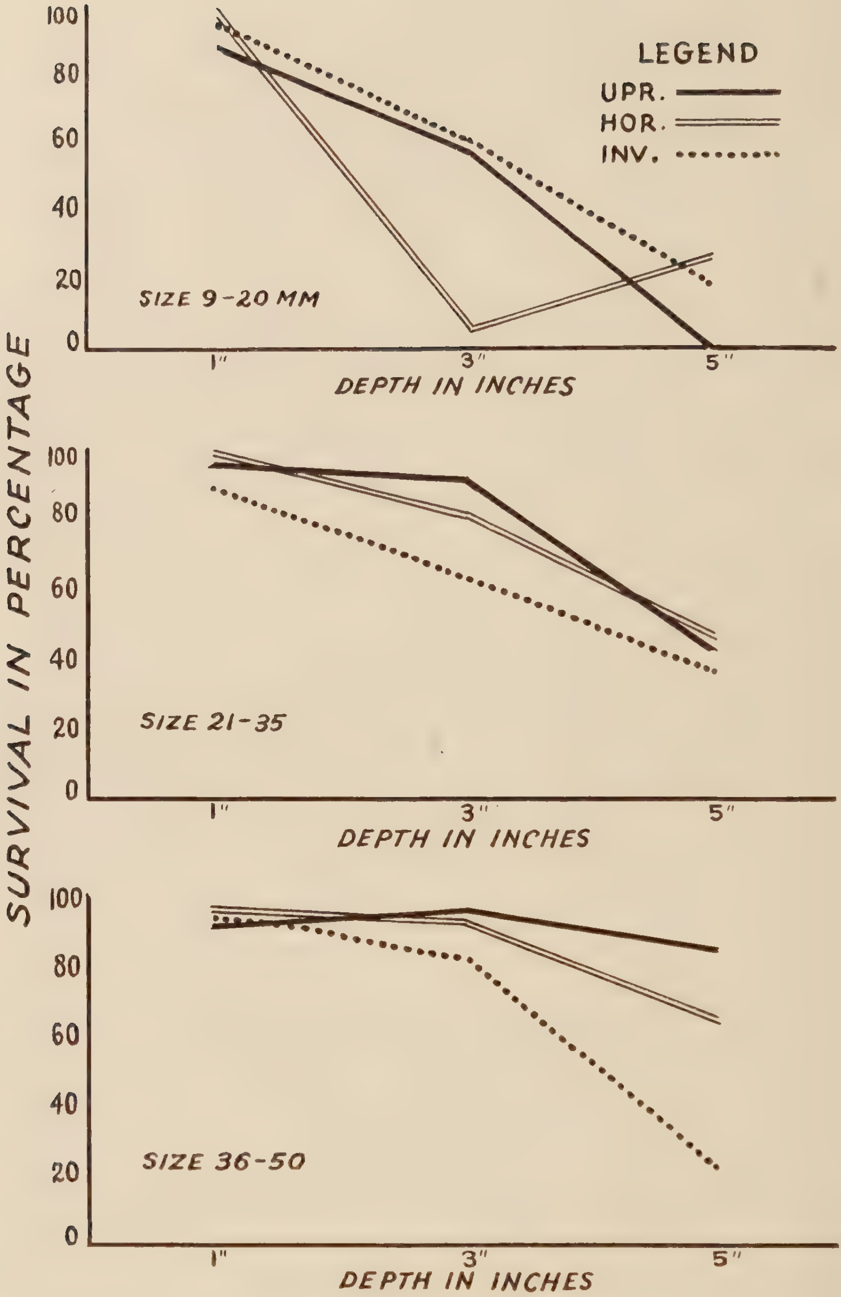

FIGURE 3 --PERCENTAGE SURVIVAL IN SANDY-MUD IN SUMMER - EXPERIMENT 3

is a serious clam predator. It is likely that these crabs crushed and ate most of the live clams of the 9-20 mm. group planted at a depth of 1 inch. This would leave few live clams but many empty shells from those which had died from the effect of the burial. Therefore, the survival percentages would be too low.

Recovery of 9-20 mm. clams at the 3 and 5 inch depths was 62.7 per cent and 75.3 per cent respectively, so results for these depths, which also indicated extremely poor survival, are considered to be more reliable than those for the 1-inch depth.

At the 1-inch depth, survival of the 21-35 mm. clams in all positions and of the 36-50 mm. clams in upright and horizontal positions was good; but survival of the 36-50 mm. clams in an inverted position was only 61 per cent. The sticky nature of the silt in this experiment is believed responsible for the poor survival of the large clams when inverted as they probably experienced difficulty in orienting themselves and many may have suffocated.

At a depth of 3 inches, the large clams in both upright and horizontal positions survived well, whereas the intermediate group showed negligible survival in horizontal and inverted positions and only 55.2 per cent survival in upright position (figure 4). Small clams generally failed to survive burial at a 3-inch depth in silt in any position.

At a 5-inch depth, only the 36-50 mm. clams planted upright had a good rate of survival (88 per cent). The next highest survival rate was for the large clams in a horizontal position (46.9 per cent). All other lots had less than 16 per cent survival at this depth.

The results of this experiment indicate that survival rate decreases as the variation from normal position becomes greater, that is, from upright to horizontal to inverted.

Table 4. — Percentage survival of clams buried in silt at various depths regardless of position — experiment 4.

Size group	Percentage survival at depth of		
	1 inch	3 inches	5 inches
9-20 mm.	18.6	1.1	0.9
21-35 mm.	76.6	26.5	6.9
36-50 mm.	83.2	73.8	48.3

Differences between survival percentages shown in table 4 were tested for statistical significance, and results are on file at the Department of Sea

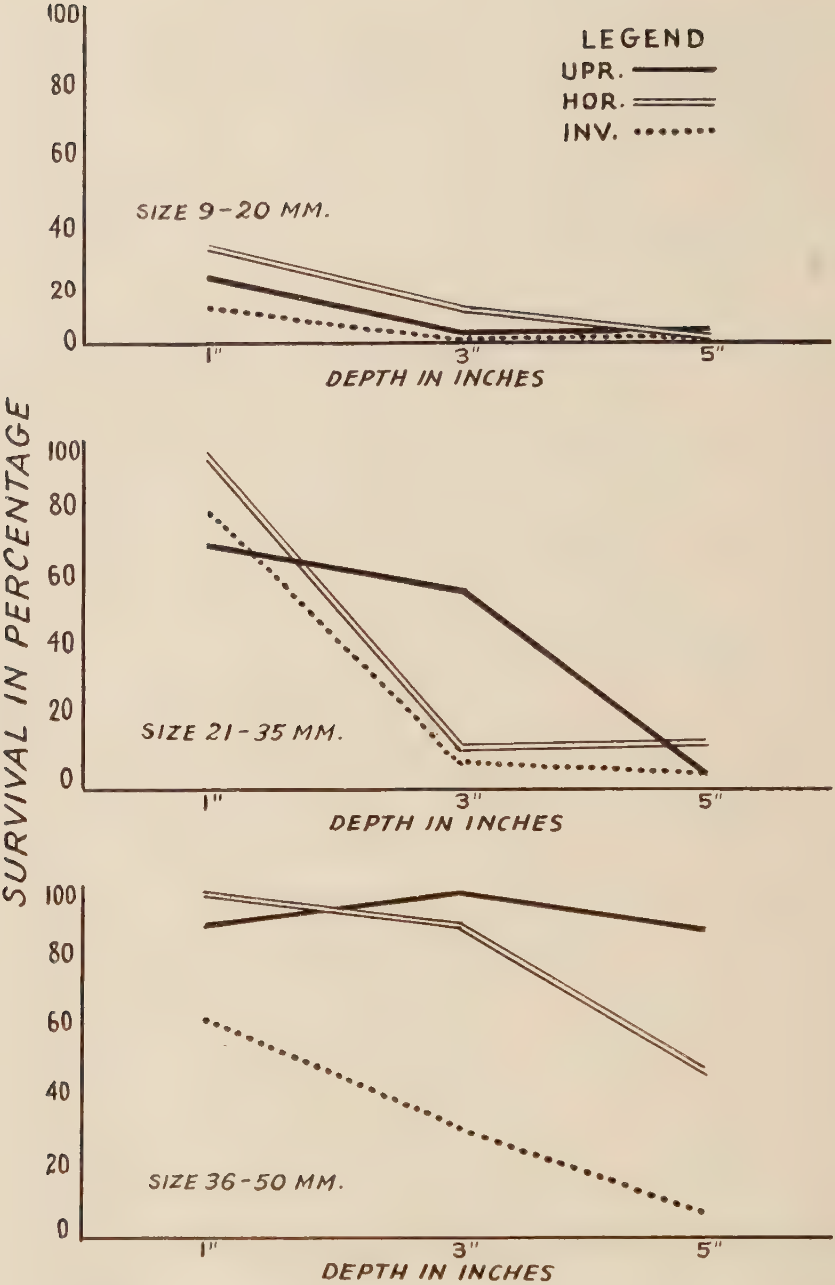

FIGURE 4 -- PERCENTAGE SURVIVAL IN MUD IN SUMMER - EXPERIMENT 4

and Shore Fisheries, Augusta, Maine. The 9-20 mm. clams survived significantly better at 1 inch than at 3 inches, but showed no significant difference between survival at 3 inches and 5 inches. Survival rates of 21-35 mm. clams were significantly different at 1, 3, and 5 inches. The difference in survival of 36-50 mm. clams at 1 and 3 inches was on the borderline of significance at 5 per cent level; however, the difference between survival at 3 and 5 inches was highly significant.

No significant difference in survival at 1-inch depth was found for 21-35 and 36-50 mm. groups. Although survival of 9-20 group at 1 inch was significantly lower than the other groups, the suspected green crab predation makes this result doubtful.

At both 3-inch and 5-inch depths, survival was directly proportional to size, with significant differences between survival rates in all cases.

Detailed records of experiment 4 are listed in table A-4 in appendix A.

Experiment 5

The fifth experiment duplicated experiment 3 except that it was conducted in the winter instead of in the summer. The clams were buried February 25, 1953, in the silty-sand of Bedroom Cove and were exhumed March 11, 1953.

Survival percentages are shown in table 5 and figure 5 and in table A-5 in appendix A.

Survival of all size groups in this experiment was good. Even at a depth of 5 inches all groups had a 60 per cent survival or over except for the smallest clams in upright position (41.5 per cent).

Summer survival in the same area was much lower as shown by experiment 3. In that experiment only two groups of clams buried 5 inches deep had over a 60 per cent survival, and these were the largest clams in upright and horizontal positions.

Table 5.—Percentage survival of clams buried in silty-sand in winter at various depths regardless of position — experiment 5.

Size group	Percentage survival at depth of		
	1 inch	3 inches	5 inches
9-20 mm.	94.9	90.0	66.7
21-35 mm.	93.6	86.9	73.0
36-50 mm.	93.2	81.8	77.4

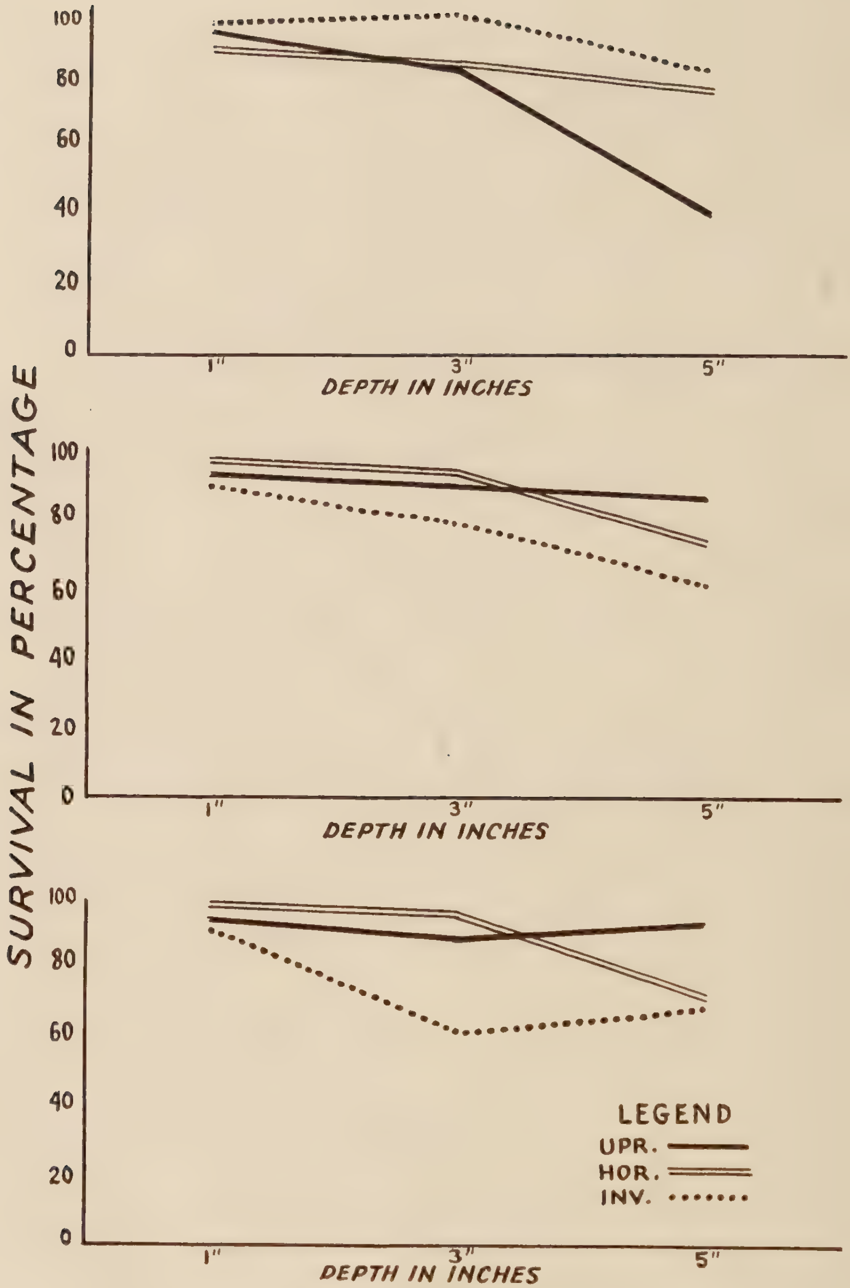

FIGURE 5 -- PERCENTAGE SURVIVAL IN SANDY MUD IN WINTER - EXPERIMENT 5

Table 5 indicates less survival as depth of burial increases. The difference between survival of 21-35 mm. clams at 1-inch and 3-inch depths was on the borderline of significance at the 5 per cent level. Differences between survival of 9-20 mm. clams at 1-inch and 3-inch depths and 36-50 mm. clams at 3-inch and 5-inch depths were not significant. All other differences between survival rates of each size group at different depths in table 5 were statistically significant. These results agree generally with those of the preceding experiments.

No significant difference in survival rates of different size groups was found in experiment 5. The relatively poor average for survival of 36-50 mm. clams at a 3-inch depth was caused by the poor survival of inverted group, 59.6 per cent. The poor average for survival of the 9-20 mm. clams at a 5-inch depth was caused by the low survival of upright group, 41.5 per cent. This experiment, like experiment 3, was conducted in firm silty-sand so burial of clams beneath a hard chunk of sediment may explain the poor survival of these two groups of clams. Table A-5 in appendix A lists the detailed records of this experiment.

DISCUSSION

Survival by depths

Average survival, disregarding position, size of clams, sediment type or season, was inversely proportional to depth as shown in the following table:

Depth	Percentage survival
1 inch	87.3
3 inches	70.6
5 inches	42.0
9 inches	3.7

These percentages were obtained from 4,106 unbroken clams recovered from all five experiments excluding plots 50 in experiment 2 and 11 in experiment 3 in which results were considered unreliable. Difference between survival percentages are statistically significant as shown by chi square tests.

These results may be compared with those of Mead and Barnes (1903) in Rhode Island, who found the following survival percentages for 32 mm. clams buried 4 days in various positions:

Depth	Percentage survival
Just covered over	94.7
6 inches	78.7
12 inches	43.5

Survival reported by Mead and Barnes might have been lower if the clams had been buried 2 weeks, as in the present experiment, instead of 4 days, and if smaller clams had been included as in the present experiment. Nevertheless, a similar inverse relation between survival and depth of burial is demonstrated by the two experiments.

Needler & Ingalls (1944) compared survival of small and medium clams buried in various positions with the following results which agree well with the present experiment:

	Percent survival	
Depth to top of clam	Small (under 1″)	Medium (1″ to 2″)
2 inches	70.0	74.0
4 inches	40.0	50.3
6 inches	10.0	38.3

Survival by positions

Average survival rates of clams planted in three positions, regardless of size, sediment type, or depth (except that 9-inch depth was omitted), were as follows:

		Percentage survival	
Position	Summer	Winter	Total
Upright	63.8	85.5	70.7
Horizontal	59.6	87.6	69.0
Inverted	41.6	79.6	55.2

Differences between survival rates in upright and horizontal positions were not significant in summer, winter, or total. Differences between horizontal and inverted, and between upright and inverted, were statistically significant.

Burial in an inverted position is much more serious to a clam than burial in upright or horizontal position. Many of the larger sub-legal clams are left inverted by commercial diggers, particularly in a firm silty-sand or silt bottom. Therefore, improvement of digging technique or restriction of digging frequency would be desirable to prevent wastage of clams.

The relation of survival to position indicated by these experiments agrees with results of Mead and Barnes (1903) who found the following percentage survival for clams buried at various depths:

Position	Percentage survival
Upright	81.0
Horizontal	64.0
Inverted	50.5

Needler & Ingalls (1944) observed the same relationship between position and survival as reported by Mead & Barnes as follows:

	Percentage survival	
Position	Small (under 1″)	Medium (1″ to 2″)
Upright	53.3	71.3
Horizontal	45.0	56.7
Inverted	21.3	34.7

Results of Needler & Ingalls' experiment which was conducted during the summer compare more closely with the results of our summer experiment than with similar tests which we made in winter.

Survival by sediment types

Clams planted in silty-sand in the summer survived better than in sand, and clams in sand survived better than those in silt, as shown in the following table:

	Percentage survival			
	1-inch depth	3-inch depth	5-inch depth	1- and 5-inch depths combined
Silty-sand	94.2	80.8	40.0	67.9
Sand	82.4	—	26.3	50.8
Silt	70.1	39.9	21.8	41.5

All differences between survival rates were statistically significant as shown by chi square tests.

Survival by seasons

Experiments 3 and 5 provided a comparison of survival in summer (July and August) with that in winter (February and March). Results in the following table show significantly greater total survival in winter than in summer. At a 1-inch depth, survival was practically the same for the two seasons; at a 3-inch depth, the difference was on the borderline of significance at the 5 per cent level. Winter survival was significantly greater than summer at a depth of 5-inches.

	Percentage survival			
	1-inch depth	3-inch depth	5-inch depth	All depths
Summer	94.2	80.8	40.0	72.0
Winter	93.9	85.7	72.8	84.2

Needler & Ingalls (1944) reported a higher percentage survival of clams left in the flats after commercial digging in late autumn and early spring than in August, but made no observations in winter.

Survival by size groups

Survival, disregarding position, depth, sediment type, and season, was directly proportional to size of the clams as shown in the following table:

Size group	Percentage survival
9-20 mm.	49.9
21-35 mm.	59.2
36-50 mm.	68.5

This comparison included 4,106 clams in the 5 experiments. The differences in the survival rates are statistically significant.

Needler & Ingalls (1944) also found survival directly proportional to size. Average survival of 1 inch to 2 inch clams, disregarding position and depth of burial, was 54.2 per cent; whereas, only 39.8 per cent of those under one inch survived.

CONCLUSIONS

1. Survival of soft-shell clams was inversely proportional to the depth of burial. Results of all five experiments involving three different sediment types and two seasons agreed with totals of all experiments in confirming this relation. Average survival, combining all sediment types, seasons, sizes of clams, and positions, ranged from 87.3 per cent at 1-inch depth to 3.7 per cent at 9-inch depth. At 3-inch and 5-inch depths, where commercial digging operations leave most of the sub-legal clams, average survival rates were 71.3 per cent and 42.0 per cent respectively.

2. Survival of clams buried in upright or horizontal positions was significantly greater than survival of those buried in an inverted position. The difference in survival rate of clams planted in upright and in horizontal positions was not statistically significant.
3. Best survival was in silty-sand; next best was in sand; poorest was in silt.
4. Average survival in winter was greater than in summer. This result was influenced primarily by the high survival rate at 5-inch depth during the winter (72.8 per cent), as compared with the summer (40.0 per cent).
5. Survival was directly proportional to size of the clams, ranging from 49.9 per cent for 9-20 mm. clams to 68.5 per cent for 36-50 mm. clams.
6. The results suggest the possibility of increasing clam production by limiting the frequency of digging. Each time a flat is dug, about half the sub-legal clams are buried too deep to survive. Others are broken by the digging operation and die. By reducing frequency of digging to the minimum required to harvest the legal clams, this mortality could be reduced and production increased.
7. The results of these experiments demonstrate the need for improved digging methods which would reduce the mortality of sub-legal clams. The first digging method, described in the introduction to this report, leaves the larger sub-legal clams close to the surface but buries the smaller clams several inches deeper. The second method leaves the smaller clams near the surface but covers the larger clams with several inches of sediment. The first method is preferable where the sub-legal population consists mainly of larger clams. The second method is better if a good population of tiny clams exists. Neither method is ideal, and neither is applicable to all types of clam flats. Further research on improvement of digging techniques is indicated.

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Appendix A

Table A1. — Summary of Experiment 1, Sagadahoc Bay (Center), Sand, 50 clams per plot buried 6/25/52; exhumed 7/11/52 and 7/14/52.

Plot No.	Depth	Size in mm.	Position	Breakage	Clams recovered Live	Dead	Total	Percentage survival
1	1″	9-20	upr	unbroken	8	0	8	100.0
3	1″	9-20	hor	”	4	1	5	80.0
5	1″	36-50	upr	”	34	10	44	77.3
7	1″	36-50	hor	”	36	10	46	78.3
9	5″	9-20	upr	”	3	5	8	37.5
11	5″	9-20	hor	”	4	24	28	14.3
13	5″	36-50	upr	”	29	19	48	60.4
15	5″	36-50	hor	”	13	35	48	27.1
17	9″	9-20	upr	”	0	12	12	0.0
19	9″	9-20	hor	”	0	17	17	0.0
21	9″	36-50	upr	”	6	36	42	14.3
23	9″	36-50	hor	”	2	45	47	4.3
25	1″	36-50	inv	”	31	9	40	77.5
27	5″	36-50	inv	”	7	43	50	14.0
29	9″	36-50	inv	”	1	40	41	2.4
2	1″	9-20	upr	broken	0	0	0	0.0
4	1″	9-20	hor	”	0	14	14	0.0
6	1″	36-50	upr	”	4[1]	37	41	2.6[3]
8	1″	36-50	hor	”	3[2]	24	27	0.0[3]
10	5″	9-20	upr	”	0	0	0	0.0
12	5″	9-20	hor	”	0	12	12	0.0
14	5″	36-50	upr	”	1[2]	35	36	2.8
16	5″	36-50	hor	”	1[2]	41	42	0.0[3]
18	9″	9-20	upr	”	0	11	11	0.0
20	9″	9-20	hor	”	0	9	9	0.0
22	9″	36-50	upr	”	0	37	37	0.0
24	9″	36-50	hor	”	0	16	16	0.0
26	1″	36-50	inv	”	1	37	38	2.6
28	5″	36-50	inv	”	0	40	40	0.0
30	9″	36-50	inv	”	0	37	37	0.0

Note: upr — upright; hor — horizontal; inv — inverted.

[1] 3 with edges chipped only slightly.

[2] edges chipped only slightly.

[3] based on broken clams only.

Appendix A

Table A2. — Summary of experiment 2; Sagadahoc Bay (Center); Sand. 50 clams per plot buried 7/3/52; exhumed 7/17/52.

Plot No.	Depth	Size in mm.	Position	Breakage	Clams recovered Live	Dead	Total	Percentage survival
31	1″	21-35	upr	unbroken	42	2	44	95.5
33	1″	21-35	hor	”	22	2	24	91.7
35	1″	21-35	inv	”	20	8	28	71.4
37	5″	21-35	upr	”	17	18	35	48.6
39	5″	21-35	hor	”	8	39	47	17.0
41	5″	21-35	inv	”	0	34	34	0.0
43	9″	21-35	upr	”	1	46	47	2.1
45	9″	21-35	hor	”	0	50	50	0.0
47	9″	21-35	inv	”	1	41	42	2.4
49	1″	9-20	inv	”	0	5	5	0.0[1]
50	5″	9-20	inv	”	0	10	10	0.0
32[5]	1″	21-35	upr	broken	6[2]	22	28	8.3[3]
34[5]	1″	21-35	hor	”	4[4]	10	14	0.0[3]
36	1″	21-35	inv	”	0	37	37	0.0
38	5″	21-35	upr	”	1[4]	42	43	0.0[3]
40[5]	5″	21-35	hor	”	1[4]	39	40	0.0[3]
42	5″	21-35	inv	”	2	40	42	4.8
44	9″	21-35	inv	”	0	46	46	0.0
46	9″	21-35	hor	”	0	41	41	0.0
48	9″	21-35	upr	”	1[4]	32	33	0.0[3]

[1] Unreliable — clams believed washed away.

[2] 4 with edges chipped only slightly.

[3] Based on broken clams only.

[4] Edges chipped only slightly.

[5] 49 clams planted instead of 50.

Appendix A

Table A3. — Summary of experiment 3, Sagadahoc Bay (Bedroom Cove); Silty-sand; 50 clams per plot buried 7/29/52; exhumed 8/12/52.

Plot No.	Depth	Size in mm.	Position	Clams recovered Live	Dead	Total	Percentage survival
1	1″	9-20	upr	29	3	32	90.6
2	1″	9-20	hor	22	0	22	100.0
3	1″	9-20	inv	31	1	32	96.9
4	1″	21-35	upr	49	2	51	96.1
5	1″	21-35	hor	48	1	49	98.0
6	1″	21-35	inv	44	6	50	88.0
7	1″	36-50	upr	48	4	52	92.3
8	1″	36-50	hor	47	2	49	95.9
9	1″	36-50	inv	38	3	41	92.7
10	3″	9-20	upr	23	16	39	59.0
11	3″	9-20	hor	2	28	30	6.7
12	3″	9-20	inv	10	7	17	58.8
13	3″	21-35	upr	42	4	46	91.3
14	3″	21-35	hor	40	10	50	80.0
15	3″	21-35	inv	25	15	40	62.5
16	3″	36-50	upr	49	2	51	96.1
17	3″	36-50	hor	50	3	53	94.3
18	3″	36-50	inv	35	8	43	81.4
19	5″	9-20	upr	0	25	25	0.0
20	5″	9-20	hor	11	28	39	28.2
21	5″	9-20	inv	6	26	32	18.8
22	5″	21-35	upr	16	24	40	40.0
23	5″	21-35	hor	19	23	42	45.2
24	5″	21-35	inv	15	27	42	35.7
25	5″	36-50	upr	34	6	40	85.0
26	5″	36-50	hor	29	16	45	64.4
27	5″	36-50	inv	12	38	50	24.0

Note: upr — upright; hor — horizontal; inv — inverted.

Appendix A

Table A4. — Summary of experiment 4, Birch Island Cove; Silt; 50 clams per plot buried 8/14-15/52; exhumed 8/28/52.

Plot No.	Depth	Size in mm.	Position	Clams recovered Live	Dead	Total	Percentage survival
1	1″	9-20	upr	4	16	20	20.0
2	1″	9-20	hor	2	5	7	28.6
3	1″	9-20	inv	2	14	16	12.5
4	1″	21-35	upr	32	15	47	68.1
5	1″	21-35	hor	20	1	21	95.2
6	1″	21-35	inv	7	2	9	77.8
7	1″	36-50	upr	42	5	47	89.4
8	1″	36-50	hor	42	1	43	97.7
9	1″	36-50	inv	25	16	41	61.0
10	3″	9-20	upr	0	47	47	0.0
11	3″	9-20	hor	1	11	12	8.3
12	3″	9-20	inv	0	35	35	0.0
13	3″	21-35	upr	16	13	29	55.2
14	3″	21-35	hor	3	18	21	14.3
15	3″	21-35	inv	3	30	33	9.1
16	3″	36-50	upr	48	1	49	98.0
17	3″	36-50	hor	44	5	49	89.8
18	3″	36-50	inv	12	31	43	27.9
19	5″	9-20	upr	1	44	45	2.2
20	5″	9-20	hor	0	45	45	0.0
21	5″	9-20	inv	0	23	23	0.0
22	5″	21-35	upr	1	37	38	2.6
23	5″	21-35	hor	5	28	33	15.2
24	5″	21-35	inv	1	29	30	3.3
25	5″	36-50	upr	44	6	50	88.0
26	5″	36-50	hor	23	26	49	46.9
27	5″	36-50	inv	4	46	50	8.0

Note: upr — upright; hor — horizontal; inv — inverted.

Appendix A

Table A5.— Summary of experiment 5; Sagadahoc Bay (Bedroom Cove); Silty-sand; 50 clams per plot buried 2/25/53; exhumed 3/11/53.

Plot No.	Depth	Size in mm.	Position	Clams recovered Live	Dead	Total	Percentage survival
1	1″	9-20	upr	46	2	48	95.8
2	1″	9-20	hor	44	4	48	91.7
3	1″	9-20	inv	41	1	42	97.6
4	1″	21-35	upr	43	3	46	93.5
5	1″	21-35	hor	46	1	47	97.9
6	1″	21-35	inv	43	5	48	89.6
7	1″	36-50	upr	46	4	50	92.0
8	1″	36-50	hor	47	1	48	97.9
9	1″	36-50	inv	45	5	50	90.0
10	3″	9-20	upr	33	6	39	84.6
11	3″	9-20	hor	32	5	37	86.5
12	3″	9-20	inv	34	0	34	100.0
13	3″	21-35	upr	43	5	48	89.6
14	3″	21-35	hor	47	4	51	92.2
15	3″	21-35	inv	36	10	46	78.3
16	3″	36-50	upr	44	6	50	88.0
17	3″	36-50	hor	55	2	57	96.5
18	3″	36-50	inv	31	21	52	59.6
19	5″	9-20	upr	17	24	41	41.5
20	5″	9-20	hor	27	9	36	75.0
21	5″	9-20	inv	36	7	43	83.7
22	5″	21-35	upr	40	7	47	85.1
23	5″	21-35	hor	36	13	49	73.5
24	5″	21-35	inv	27	18	45	60.0
25	5″	36-50	upr	48	4	52	92.3
26	5″	36-50	hor	33	13	46	71.7
27	5″	36-50	inv	39	18	57	68.4

Note: upr — upright; hor — horizontal; inv — inverted.

THE TIDAL SPAT TRAP,
A NEW METHOD FOR COLLECTING SEED CLAMS

John B. Glude

U. S. Fish and Wildlife Service, Boothbay Harbor, Maine

The Fish and Wildlife Service was directed by Congress in 1948 to determine the causes of the decline of soft and hard-shell clams along the Atlantic Coast, and to develop methods for increasing production. Our initial approach was to accept, for the time being, the statements that a scarcity existed and to attempt the most logical method for increasing production, viz., clam farming.

Clam farming is a well established practice in a number of parts of the world and it seemed reasonable that methods which had been used in other places might be applied to the New England Coast. For many years the Japanese have utilized the tidal flats in Tokyo Bay for the production of clams as a farming venture (Glude, 1947). This industry is based on the collection of seed clams from the flats at the mouths of several rivers and the transplanting of these clams to private grounds. After a growing period of about one year the clams are dug and sent to market.

Another commercial clam farm exists in Puget Sound, Washington, where one concern has title to approximately 10 miles of beach. Reproduction appears to be adequate on these flats and the entire farming procedure depends on natural seeding of the flats. In this case clam farming approximates the management of forestry land where it is simply a matter of harvesting a crop as it comes along and then leaving the area until a new crop has reached commercial size.

The third area where commercial clam farming is practiced is the eastern shore of Virginia. (Tiller, Glude, Stringer, 1952). Here small hard-shell clams are placed on private beds, protected from predatory fish, and marketed when they have attained sufficient growth and when economic conditions are favorable. In each of these clam farming ventures the primary requirement is a source of seed. Therefore, we have devoted a considerable amount of our effort to a search for a source of juvenile clams.

We recognize three principal methods of obtaining seed clams.

1) Collection of juveniles which have naturally set in large numbers,
2) Artificial propagation,
3) Collecting spat or juvenile clams by some device.

Natural setting appears to be the most practical method for the collection of soft-shell clams. We have found one place in Maine where each year soft-shell clams, 1/2 to 1 inch in length are found in concentrations of 1,000 to 1,200 per square foot over a considerable area of sandy beach. We have developed methods for collecting these small clams by sorting them from the sand using a hydraulic seed rake (Glude, Spear, Wallace, 1952).

Young hard-shell clams, on the other hand, are seldom found in heavy concentrations. Ordinarily our bottom samples in Rhode Island contain one to 20 per square foot and it is difficult to work out mechanical methods for removing clams when they occur in these low concentrations. Only once in Rhode Island have we found hard clams in concentrations which might be usable as a seed source. This instance occurred in Greenwich Bay in the summer of 1951 when some of our samples contained as many as 600 _Venus_ per square foot. This, however, appeared to be a very unusual instance and could not be depended upon as a source of seed quahaugs for a commercial farming venture.

The best natural source of juvenile hard shell clams which we have seen is in Casco Bay, Maine. The Maine Department of Sea and Shore Fisheries is now transplanting these overcrowded and stunted clams to deeper waters where they will grow faster and where they will be protected from freezing (Dow and Wallace, 1951). These clams set during recent years when temperatures have been high. A cold cycle might prevent _Venus_ from reproducing in Maine. Therefore, we consider natural setting as a sporadic source of seed which should be utilized when available, but which can not be depended on each year.

Artificial propagation has long been the goal of both oyster and clam biologists. Reliable methods for propagating _Venus_ have now been developed by Dr. Loosanoff and have been applied in several laboratories. Hard-shell clams, fortunately, are among the easier bivalves to rear and this method may some day be usable on a commercial scale. It is entirely possible to rear soft-shell clams in a hatchery, but since they are so often available from natural setting it would probably be more economical to use this source of seed rather than artificial propagation.

The third method of collecting seed is that of employing some device or procedure to induce setting or of collecting the young juvenile clams. In the oyster industry this would include spreading shells on the bottom to catch the set. In Japan, it might consist of hanging fibre mats out in the water to which the young larvae of some of the clams would attach. We have tried a great number of methods of inducing setting, some of which have been successful and most of which have failed. A timely suggestion from Roger Munsey, who was then

President of the Massachusetts Shellfish Officers' Association, led us to design an automatic filtering device which we have named the Tidal Spat Trap.

The Tidal Spat Trap is simply a box which fills and empties with the tide and a system of check valves to force the outgoing water through a sand filter. The bivalve larvae are carried into the box by the incoming tide and are kept there by a tray of sand which filters the water on its way out. The outlet is located about eight inches above the filter so the larvae and spat can remain in water even though the tide falls below this level. Figure 1 is a diagram of the operating principle of this device.

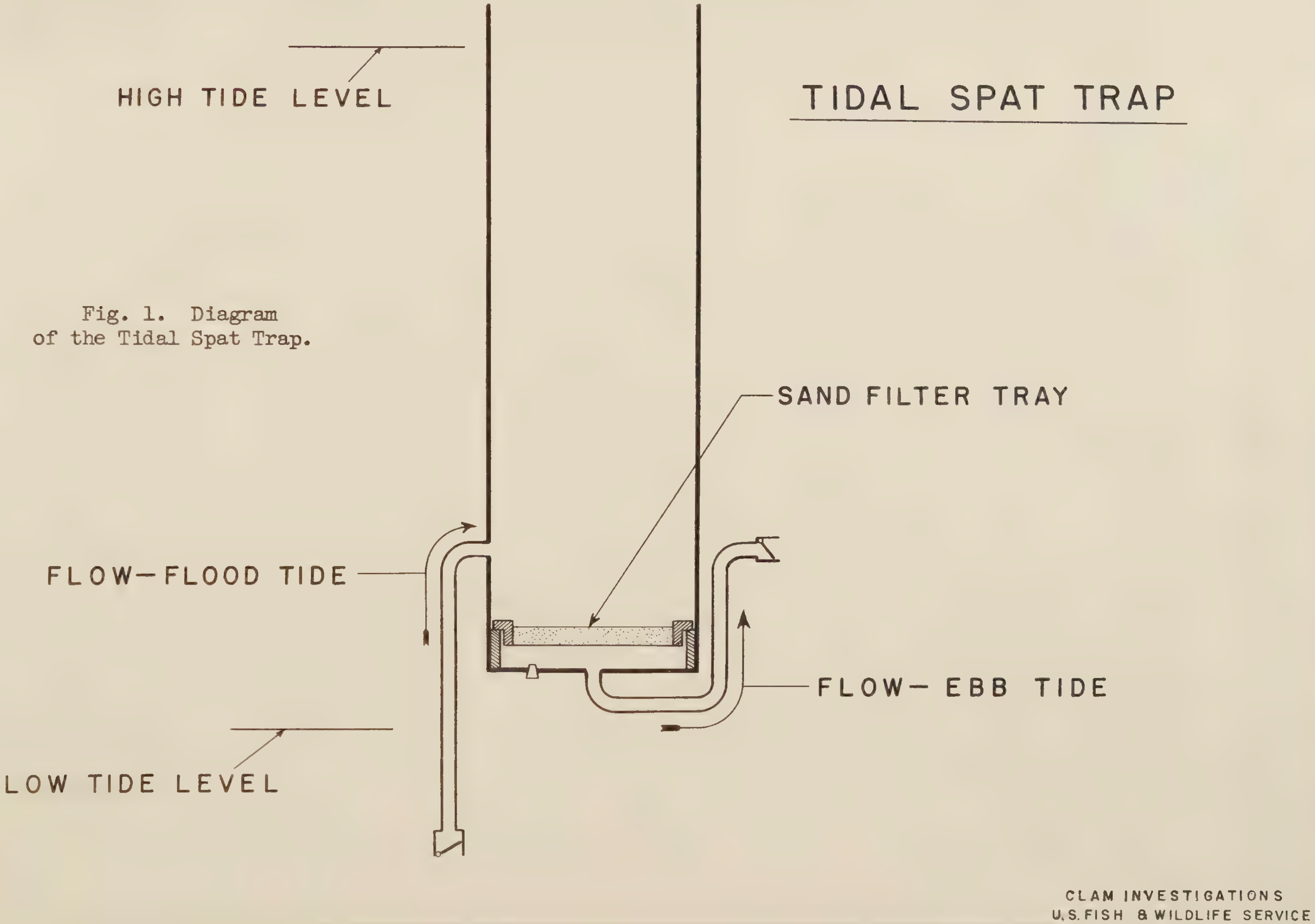
TIDAL SPAT TRAP
HIGH TIDE LEVEL
SAND FILTER TRAY
FLOW—FLOOD TIDE
FLOW— EBB TIDE
LOW TIDE LEVEL
CLAM INVESTIGATIONS
U.S. FISH & WILDLIFE SERVICE

Fig. 1. Diagram of the Tidal Spat Trap.

Results, 1953

The first Tidal Spat Trap was installed at Boothbay Harbor, Maine in May, 1953, to test its operation. Table I shows the number of bivalves caught in the sand filter during the first month. The trap caught over 10,000 bivalves per square foot of sand filter in the first 24 days. Of these, nearly a thousand were soft-shell clams. The ratio of mussels to soft-shell clams was about what we expected from plankton samples.

Table I: Catch of Bivalves per Square Foot of Sand Filter. Mark I Tidal Spat Trap, Boothbay Harbor, Maine 1953

Date	No Days	Soft Clams	Total Bivalves
May 26	Trap installed.		
June 4	8	---	2,000
June 12	16	648	6,372
June 18	22	952	10,639
June 18	Sand filter changed.		
June 19	1	73	1,171

On June 22 we transferred the spat trap from Boothbay Harbor to Robinhood Cove and attached it to the side of an old sailing ship which had been beached there. This location proved to be less suitable than the wharf at the Boothbay Harbor Laboratory because of the large amount of silt in the water which tended to plug the sand filter. In spite of the plugging by silt, the trap continued to catch bivalve larvae in fairly good numbers as long as they were present in the water.

The sand filters were taken from the spat trap at intervals and placed in running water at the laboratory. Periodically, the number of juvenile clams and mussels in these trays were checked. We found that nearly all of the mussels died after they were brought to the laboratory; whereas, many of the clams survived. By October the soft clams present in the tanks ranged from 2 to 9 millimeters in length which we considered very good growth in comparison with naturally set juvenile clams.

The spat trap was also tried as a plankton collector by replacing the sand filter with a plankton net tray made from No. 18 triple extra heavy plankton netting. This proved to be quite successful in straining bivalve larvae from the water until the plankton net plugged. We found that the net would filter successfully for about two days which would represent four tides or about 700 gallons of water. It appears that the spat trap might be useful in some places as an intermittent plankton sampler since it filters all of the water which is taken during each incoming tide.

Results, 1954

During the winter, two additional spat traps were designed and built. The Mark II, or Maine model, is 2 feet square and 10 feet tall, to accommodate tidal ranges of 8 to 10 feet. The Mark III, or Rhode Island model, is 5 feet high and has a cross section of 2 feet by 4 feet. This trap is designed for tidal ranges of 4 to 5 feet.

In June, 1954, the three spat traps were put into operation. The Mark I, or original model, was placed at Loves Cove on Southport Island, Maine which is the area where we are now conducting most of our plankton studies concerning soft-shell clams. The Mark II spat trap was installed in Orr's Cove, Maine, which contains a large population of hard-shell clams and is noted for its heavy sets. This cove was chosen as a typical area in Maine where hard-shell clams are found.

The Mark III spat trap was installed at Wickford, Rhode Island, on June 2, 1954, and placed in operation the following day. Mechanical difficulties with the check valves prevented its successful operation until June 10. Following this time the check valves and filters operated successfully and *Mya*, *Venus*, and *Mytilus* larvae began to appear in the samples which were taken.

Table II shows the catches of larvae and spat by the Loves Cove spat trap during June and July of 1954. Few larvae were present in the water during the period from June 10 to July 2 and this accounts for the low numbers of mussels and clams that were obtained by the trap during this period. Following that time the number of clam larvae in the plankton increased which resulted in fairly good catches by the trap during the following week. Highest catch recorded to date was for the period from July 9 to 12 when over 400 soft clams were caught by each square foot of sand filter in the trap. In a commercial operation of a spat collecting device such as this, the most productive period would be during times like that from July 9 to 12 when large numbers of mature larvae are present in the water.

Table II: Catch of Bivalves per Square Foot of Sand Filter. Mark I Tidal Spat Trap, Loves Cove, Maine, 1954.

Date	No Days	Soft Clams	Total Bivalves
June 10	Trap installed.		
July 2	22	93	162
July 7	27	139	789
July 9	29	464	1,995
July 9	Sand filter changed.		
July 12	3	418	627

The best catch to date of the Mark II trap at Orr's Cove was during the period of July 15 to 19. In these four days each square foot of filter caught 1,044 _Venus_ larvae and spat. The total catch of bivalves was 2,396 per square foot. The location of this trap appears to be very favorable since a strong current flows past it during the flooding tide.

The Mark III spat trap at Wickford, Rhode Island, has twice the filter area of the Mark I and Mark II traps. Therefore catches of spat per square foot of filter are expected to be lower. Best results to date were obtained during the week before July 19 when each square foot of filter caught a total of 5,296 larvae of which 656 were _Venus_. At this time plankton counts averaged 172 _Venus_ per hundred gallons of water.

From July 19-22 the Wickford trap caught only 48 _Venus_ per square foot of filter, but plankton samples averaged only 6 per hundred gallons during this period. It appears that the spat trap catches follow closely the abundance of larvae in the water.

Conclusions

1. The principles involved in the design of the Tidal Spat Traps are sound.

2. Mechanical difficulties have been overcome. The only moving parts of the spat trap are the two check valves which have been found to operate satisfactorily. The sand filter retains larvae and spat and allows the water to pass through. No outside power source is required.

3. The results depend on the location, time, and presence of advanced or mature larvae. The location in Orr's Cove appears to be satisfactory; whereas, the location of the Mark I trap in Robinhood Cove last year was unsatisfactory because of the silt and sediment in the water. The Loves Cove spat trap this year may not be in the best location possible since it is in a cove where there is little circulation of water. The maximum catches indicate that this device may have commercial potentialities for hard-shell clams.

4. Methods for holding the seed until it grows to a size when it can resist predators are now needed. This is the next project. We have tried holding the spat in the laboratory at Boothbay Harbor but have found that we would have insufficient room although the growth and survival appear to be satisfactory. Perhaps screened or fenced plots could be developed where the seed could be planted until it had reached a sufficient size. It may also be possible to find certain areas which are free from predators. Growth plots could be established in such areas and the seed transplanted to their final grounds after they had reached a large enough size to resist predators.

5. We can visualize several applications of the Tidal Spat Trap when the details of its operation are perfected. It could be used in Rhode Island to obtain seed which could be planted along the Maine Coast during cold cycles when there was no natural reproduction in Maine. The spat traps might also supply seed for private hard clam farms. Biologists could use this as a research tool for evaluating the success of setting or for determining the amount of plankton in the water.

6. This description has been presented as a report on an applied research project which is now in progress. A complete evaluation of the Tidal Spat Trap will be given when the present tests are completed.

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1955 Pink Salmon Prospect

Southeast Alaska Fingerling Census Will Fill Gap in Data

By **MITCHELL G. HANAVAN**

EDITOR'S NOTE—This article is a portion of a longer paper by Mr. Hanavan, U.S. Fish and Wildlife Service biologist, discussing The Annual Census of Young Pink Salmon as steps toward a reliable "Prediction of Abundance" for the Southeast Alaska fishery. His work is concerned primarily with the data obtained as to the adult spawners and resulting fry at six Southeast Alaska streams where adult/fry census stations are maintained. This season, as Mr. Hanavan relates, the industry is cooperating in a study of Pink salmon fingerling abundance as observed at 100 salmon traps.

● Success of the Southeast Alaska Pink salmon fishery in 1955 will depend upon the ability of a woefully small brood to gain in strength through favorable survival rates.

Fry counts at the Herman and Snake Creek adult-fry census stations operated for 7 years by the U. S. Fish and Wildlife Service in Southeast Alaska indicate that an initial gain of substantial proportions *did* occur in the early-run stocks. Both streams show exceptionally high fresh water survival rates, and fry production equal to that of the 1952 brood.

Late-stream production is less encouraging. Katlian census station shows poor survival, while at Old Tom, Harris and Sashin Creeks survival rates were fair. As a result, fry production at Old Tom, Harris and Katlian declined sharply from the 1952 level.

A similar comparison cannot be made at Sashin Creek since the even year run was eliminated in 1950 when it reached a very low abundance level. (In even years Sashin Creek is now used as a barren stream to measure the straying of Pink salmon.)

● *FINGERLING CENSUS*—This is little evidence in the Sashin Creek record of a compensatory relationship between fresh water and marine survival rates. At population levels of recent years they appear to be independent of one another, and equally variable. Combined records of other census stations, however, indicate that a compensatory relationship may exist, i. e., the greater abundance of fry from the 1950 and 1951 broods suffered the heavier marine mortalities.

We assume that to achieve accuracy in predicting returns we must have a measurement of marine survival or a measurement of Pink salmon population at a stage in the marine cycle following the period of the greatest variation in ocean mortality. As we know little of the marine history of our salmon we have no precise knowledge of the causes for the drastic changes in survival that occur from year to year, nor of the period of marine growth during which the mortality rate is most variable.

However, since mortality rates are greatest during early life, it is reasonable to believe that the greatest changes in abundance levels occur in the first few weeks after the fry emerge from the gravel. During this period the fry completes the transition from the fresh water to the marine environment, feeds voraciously, and develops a strong protective schooling habit. By late summer it grows from an initial length of 1¼" to a length of 4 or 5" and becomes less vulnerable to many of the smaller predators. Undoubtedly a considerable portion of the total marine mortality occurs during this relatively brief period, and it is entirely possible that the level of abundance established in these first few weeks will show a closer relationship to the abundance of adults than to the abundance of fry.

● *INDUSTRY COOPERATING*—To explore this possibility the Fish and Wildlife Service, with the cooperation of the fishing industry, will undertake an annual census of Pink salmon fingerlings. This program during the summer of 1955 will include daily observations at more than 100 fish traps in Southeastern Alaska. Supervision will be provided by experienced fishery biologists to assure a uniform basis for estimates of abundance and accurate identification of the young salmon.

Over a period of years abundance estimates obtained in this manner may provide an essential link in our series of population measurements. We shall then have three inventories of each of our Pink salmon broods:

First, the record of catch and escapement. Since these two measurements fluctuate in a similar pattern either may be used as an index of abundance. Escapements are the preferred index, however, as they indicate variations in spawning distribution as well as abundance.

Second, is our fry production measurement which indicates the initial success of our populations in relation to their time of spawning and to the area in which they spawn. Greater precision in the evaluation of environmental influences in fresh water survival

Sashin Creek Pink Salmon Census Data

Brood Year	Spawning Escapement	Fry County	Fry/eggs (F.W. Survival)	Returning Adults/Fry (Marine Survival)
1940	53,594	3,402,830	6.4	2.7
1941	84,304	1,024,364	1.2	1.4
1942	92,085	674,672	0.8	0.6
1943	14,983	227,673	1.5	2.4
1944	4,176	104,113	2.7	0.9
1945	5,465	41,900	0.8	3.5
1947	1,486	(1) 26,454	2.0	11.1
1949	4,902	176,025	3.7	2.5
1951	4,336	379,585	9.3	0.3
1953	1,164	94,531	~~1.7~~ 7.0	
	Average Survival Rates		3.55	2.82

NOTE—Data for Fresh Water Survival and Marine Survival are given in percentages. In other words, the percentage of the eggs carried into the stream represented by the migrating fry of the following spring; and the percentage of the fry migration of one brood which returned to the stream as adults.
(1) Plus 17,600 hatchery-reared fry from another stream.

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rates should emerge from these and related measurements of flow, temperature, and other elements in the environment.

Third, population estimate, that of fingerling Pink salmon, should provide a forecast of adult abundance more precise than either the first or second, and should also indicate severity of early marine mortality, the major causes of which may then be identified and measured.

Together, the fry and fingerling censuses may provide an index of adult return, and an indication of the areas which will receive the greater returns.

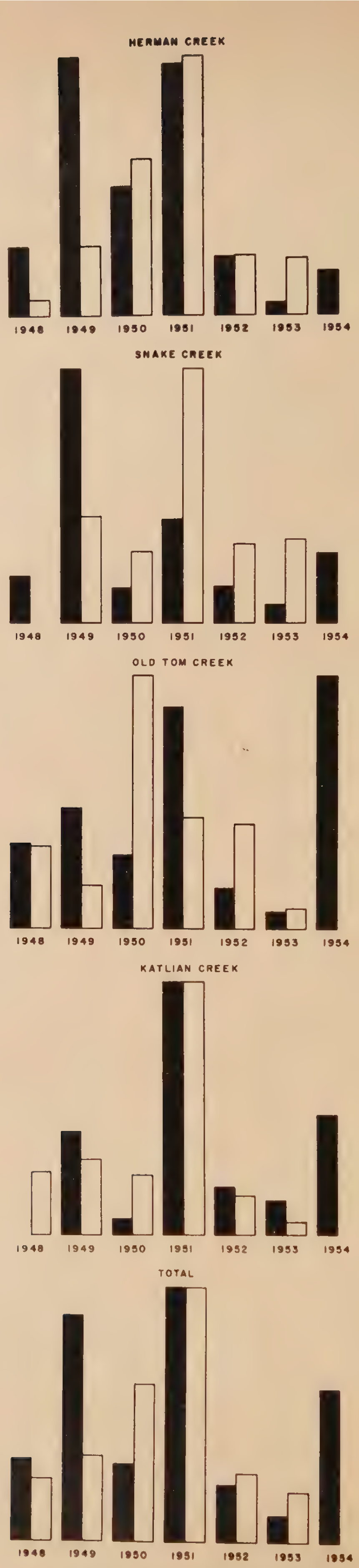

Figure 3 - Abundance of adult (solid bar) and fry (open bar) pink salmon at four Southeastern Alaska counting stations.

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LANDING LARGE YELLOWFIN—Two men landed all fish, retrieved buoys, and put droppers on racks. Photograph by G. I. Murphy

By EDWIN S. IVERSEN
and
GARTH I. MURPHY

The authors are fishery research biologists on the staff of Pacific Oceanic Fishery Investigations, who accompanied the vessels on the trips which they discuss.

It is noteworthy that the **North American** was reported wrecked on Point Loma, near San Diego, early in November, 1954.

What the Jangaard Longline Venture Found in Mid-Pacific

● During a recent commercial fishing trial of central Pacific tuna waters by two West Coast fishing boats, a total catch of 210 tons of Yellowfin tuna was landed at Honolulu and San Diego. This fishing was done in equatorial grounds previously explored by research ships of the Pacific Oceanic Fishery Investigations (POFI), a branch of the U. S. Fish and Wildlife Service in Hawaii. These commercial vessels, under contract with the Service, were given financial assistance to purchase fishing gear and make vessel alterations, and the fishermen undertook to test thoroughly the commercial possibilities of this potential fishery using two vessels to fish tuna longlines on a total of four trips. POFI biologists were aboard the boats on both sets of trips, and the following account is based on their observations.

● *FIRST CRUISES*—On the evening of January 12, 1954, the *North American*, an 86′ bait boat skippered by Capt. Sverre Jangaard, and the *Alrita*, a 70′ combination boat captained by Capt. Lars Jangaard, departed San Diego for the tuna grounds near the Equator in the vicinity of Christmas Island.

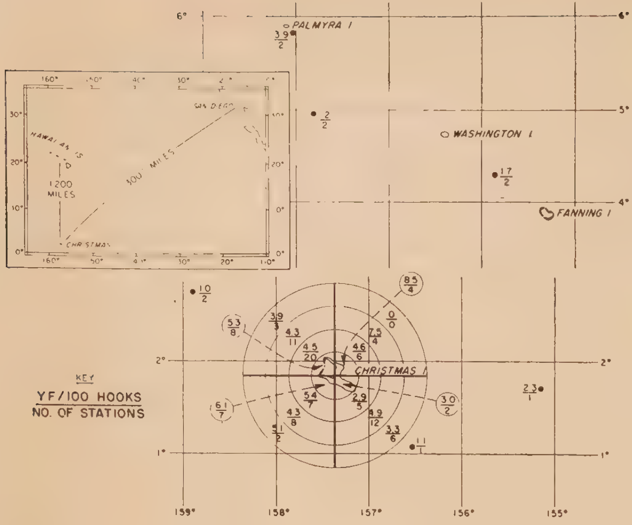
After about a month of fishing the two vessels put in at Honolulu, where they unloaded 103 tons of Yellowfin tuna at Hawaiian Tuna Packers, Ltd. Over 4 tons of market fish, including marlin, Bigeye, wahoo, and shark, was sold fresh at varying prices on the local market.

In all, the *Alrita* fished 31 days and the *North American* 30 days during the period January 27 to February 28, although the first few days of fishing were spent mainly in experimenting with the gear and methods of handling it. Once the vessels settled down to serious fishing, they averaged 57 baskets (855 hooks) of longline gear per day for the first set of cruises.

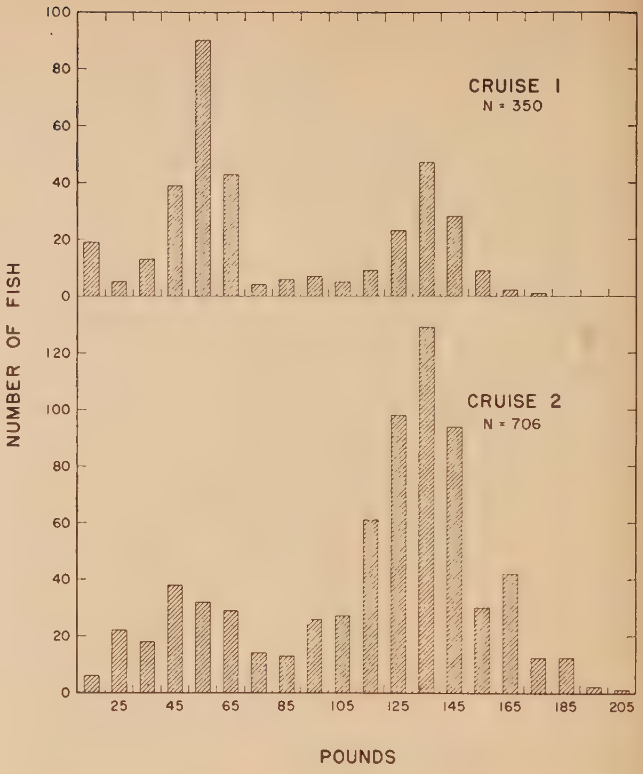
It is significant that on all but two or three days the two boats fished near each other. It had been planned originally that they would keep close company only during the first few days, while the fishermen were familiarizing themselves with this type of fishing. From the outset, however, difficulties arose in the form of numerous breaks in the main lines due to the use of excessively lightweight fiber line and to the setting of gear across current rips in unfamiliar waters; for these and other reasons the two boats continued to fish within sight of each other. Somewhat of a handicap was thus imposed, for had the vessels separated during those periods when fishing was poor, they would have been able to scout a greater area, possibly increasing their catch by more rapidly finding new concentrations of fish.

● *TWO TYPES OF FISH*—Generally, the Yellowfin consisted of two size groups. The smaller averaged about 55 lbs. and were designated "school fish" since their capture was always accompanied by signs of Yellowfin at the surface. The other group of fish averaged about 135 lbs. and were recognized as "deep-swimming Yellowfin," in that they were not seen at the surface and were captured both with and without surface signs of fish.

There was considerable fluctuation in the catches from day to day, but underlying these short-term variations there seemed to be three different periods in the fishing. The first, from January 27 to February 8, afforded moderately good fishing, with the best daily catch per boat amounting to about 3 tons. The second period, from February 9 to 15, saw very good fishing, with a high day's catch of 9 tons



Where They Fished— And What They Caught



by the *North American.* Finally, catches dropped back again to the earlier level, with the best catches ranging up to 3 tons. During the two periods of moderately good fishing the catch comprised large numbers of "school fish" with moderate numbers of "deep-swimming tuna." During the middle part of phenomenally good longline fishing the Yellowfin population around Christmas Island appears to have been augmented by an influx of large numbers of "deep-swimming tuna" that later left the area.

Summarizing the catch of the first trip to the equatorial grounds, in 30 fishing days the two vessels combined captured 2,512 Yellowfin tuna weigh-206,110 lbs. The average daily catch was 1.75 tons of saleable Yellowfin per vessel.

In addition to the 103 tons of Yellowfin that was delivered to the cannery, there were 298 Yellowfin damaged by sharks. Some of these were completely consumed except for the head, but others that were only slightly damaged were delivered to Honolulu and sold on the fresh fish market. The tuna delivered to Hawaiian Tuna Packers was processed into solid, chunk, and grated packs. Most of the fish were satisfactory for these standard packs, but in the judgment of the canners some were unsuitable and a 15% deduction was assessed against the loads. Most of the rejected fish were judged by Hawaiian Tuna Packers to be either too dark or too "green" for a light meat pack.

- *GEAR OPERATED*—The amount of gear fished was remarkable, considering that there were only seven men aboard each of the vessels. Because of the numerous breaks in the main lines, the captains did not want to chance having inadequately lighted gear out after dark, and the small number of buoy lights available, four on each vessel, was partly responsible for the limitation of the size of sets to a maximum of 70 baskets of longlines. Furthermore, the long baskets (1,620′ main lines with 15 hooks) offered more resistance to the water than the 1,260′ main lines and 11 hooks of the baskets normally fished by POFI research vessels; thus hauling was slower, averaging 26 seconds per hook as compared with 20 seconds per hook with POFI gear.

The gear used by the Jangaards was an adaptation of the most recent type of longline developed by POFI, the only essential difference being the longer main line and the increase in the number of branch lines from 11 to 15. One reason for lengthening the main line was to make the gear fish deeper; POFI results show that often the deeper hooks catch the most Yellowfin. During this cruise 46% of the Yellowfin were taken on the five deepest hooks, apparently justifying the increased main line length. However, the long baskets were hard to haul because of their greater weight. This put more strain on the line and the winch and appeared to slow-down the hauling process, particularly when several fish were caught on a single basket.

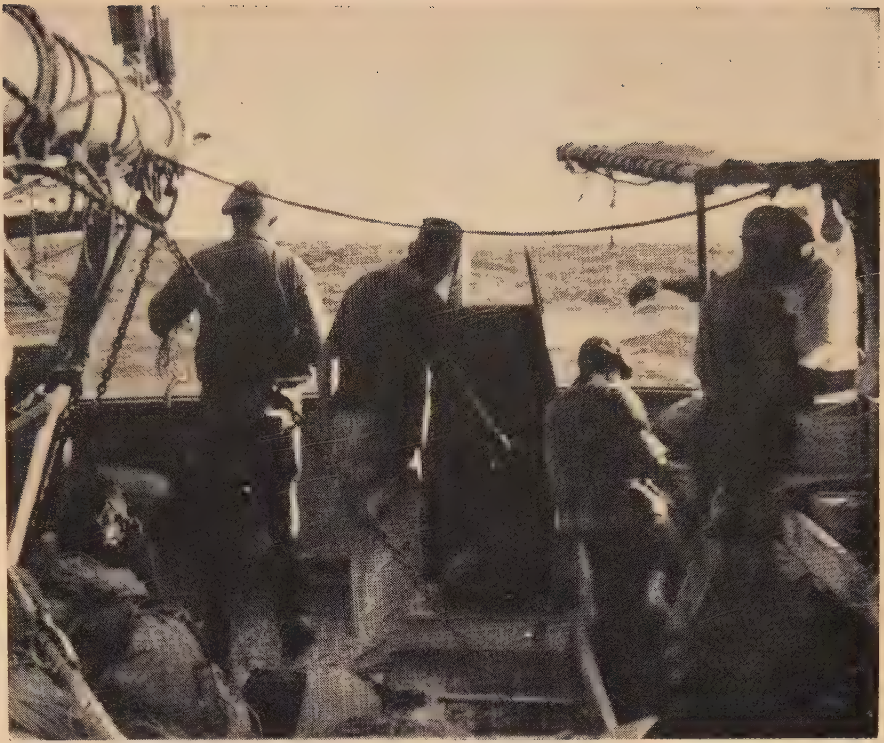
The gear was set and hauled in virtually the same manner as used by Japanese fishermen and aboard POFI vessels, except that one significant modification permitted a crew of only seven men to carry out the entire operation. (The Japanese use up to 30 and POFI uses 9 or 10). This was the practice of not coiling the droppers in with the main line when the baskets were retrieved. The branch lines were made as short as possible, only 1 fathom of cotton line and 1 fathom of wire leader, and a rack was devised that would hold 60 branch lines and keep them clear during stowage. During hauling, the branch lines were stowed on these racks as they were unsnapped from the main line, and the main lines were stowed in canvas skates. In stowing the main lines the metal links to which branch and float lines are attached were arranged so they could be easily found. On setting, the gear was assembled as the main line paid out, branch lines and float lines being snapped in as needed. This system called for more work during setting than if the branch lines were left snapped-in and coiled down with the main lines, but it considerably lessened the work during the critical hauling period.

The fresh-frozen Alaska herring used as bait were double hooked, through the eye and back through the shoulder, in order to reduce the loss of bait during the soaking period.

- *SECOND CRUISES*—After selling the first catches in Honolulu, the two boats refuelled, provisioned, and sailed again on March 13 for the Line Islands area. Fishing began on March 18 and was continued for 20 days by the *Alrita* and for 40 days by the *North American.* On April 7 the *Alrita* departed Christmas Island and arrived at Honolulu on April 15 while the *North American* departed Christmas Island April 28 and arrived at San Diego on May 15. There were no changes in the gear or fishing methods on the second set of cruises. The average numbers of baskets set per day were 63 (945 hooks) for the *Alrita* and 62 (930 hooks) for the *North American.*

The total catch of the *North American* on this trip consisted of 1,728 Yellowfin, 8 Bigeye, 64 Skipjack, 8 Albacore, 41 black marlin, 511 shark, and a few miscellaneous fish. Tuna landed at San Diego amounted to 72 tons. The *Alrita* caught 689 Yellowfin, 22 Skipjack, 9 Albacore, 7 Bigeye, 16 black marlin, 216 shark, and some miscellaneous fish. Of the 35 tons of tuna and about 7 tons of marlin landed at Honolulu by the *Alrita,* about 10 tons of Yellowfin and some of the marlin had been transferred from the *North American* when it became necessary for the smaller vessel to leave the fishing grounds after 20 days of fishing. The *North American* had an average catch rate of 4.4 Yellowfin per 100 hooks per day. Of her Yellowfin catch, 248, or about 14%, were mutilated by sharks. The *Alrita* averaged 3.6 Yellowfin per 100 hooks and had 12% of them damaged by sharks.

In general no such difference in the capture of fish by the deep and shallow hooks, as was seen on the first cruises, could be detected. The catch of Yellowfin per 100 hooks at the few stations away from the island was lower (averaging 1.9 fish per 100 hooks), and no particular area in the vicinity of the island seemed better than any other. The Yellowfin catch appeared to consist of at least two size groups, one weighing about 50 lbs. and the other about 130 lbs. The average weight of all Yellowfin taken on the cruise is estimated at 110 lbs. More males were captured than females, the ratio being 54% males to 46% females when all sizes are considered.



SETTING LONGLINE on the **Alrita.** The coiled mainline was set under the chute and allowed to pay out with slack thrown periodically by hand. The man on the left handled buoys and poles. The three men on the right cleared, baited, and snapped on droppers. Photograph by G. I. Murphy.

The *Alrita's* catch was sold in Honolulu to Hawaiian Tuna Packers. Of the approximately 70,000 lbs. of Yellowfin landed, the deduction to the fishermen was 6,109 lbs. or a 9% loss. A large portion of the catch was packed as smoked tuna. Although the fresh market demand was poor, some of the market fish were sold locally.

The *North American's* catch was landed at the Van Camp Sea Food Company in San Diego, Calif. The cannery reported the weight as 144,316 lbs., including a few shark-damaged fish. Rejections of cooked and cleaned fish by the cannery were observed; no honey-combing was seen, the majority of the rejects being "green" and a lesser amount too dark in color. The total deduction was 36,162 lbs. or about 25% of the load. The catch was packed as "bite size" with the exception of a very small portion that was put up as flakes.

The weight of fish delivered constituted a capacity load for each vessel. The large Yellowfin did not stow handily so cargo space utilization was poor, and furthermore some of the brine tanks were needed to hold fuel for the *North American's* return trip to San Diego.

Two Gilbertese natives from Christmas Island, one of whom spoke English, were employed when one of the *North American's* fishermen left the ship. They were paid $2.60 for 8 hours work, after which they are entitled to overtime. Employment is being sought for these people and the Christmas Island Plantation encourages their use.

The *Alrita's* fishermen shared about $2,100 for 51 days of fishing or 93 days at sea. Shares on the *North American* were about $3,100 for 70 fishing days or 117 days at sea. Without government aid the *Alrita* shares would have been around $1,100 and those of the *North American* about $1,700.

- *WHAT WAS LEARNED*—In unfamiliar waters the seven-man crews from these two vessels successfully adopted a fishing technique heretofore used only by Japanese on vessels with 20 to 40 fishermen. On the first set of cruises each of the vessels averaged about 1.75 tons of Yellowfin per day of fishing and on the second set about 1.78 tons. There was an increase in the average weight of the Yellowfin captured from 80 lbs. on the first cruises to 110 lbs. on the second set. Although it has not always been the case on POFI research cruises, the commercial boats found better fishing close to Christmas Island (within 60 miles) than at greater distances. The variability of the catch from day to day was so great that it was not possible to detect any clearly superior fishing grounds around the island. No fishing time was lost because of bad weather during the entire period of these cruises.

From these results it is to be concluded that it is commercially practicable for American fishing boats, using reasonably small crews, to fish Yellowfin tuna in the equatorial central Pacific by the longline method.

Annotated List of Birds Observed on Christmas Island, October to December, 1953

JOSEPH E. KING

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January, 1955

Annotated List of Birds Observed on Christmas Island, October to December 1953

JOSEPH E. KING[1]

IN OCTOBER 1953, the Pacific Oceanic Fishery Investigations of the U. S. Fish and Wildlife Service landed a small field party (the author and Mr. Richard Shomura) on Christmas Island for the purpose of installing weather instruments and sea thermographs, and to conduct a tuna bait-fish survey of the lagoon. We were on the island from October 23 to December 9, 1953, and although our time was generally occupied with the duties mentioned above, we had many opportunities to observe the interesting bird life of the island. As Christmas and other islands of the Line Island group (Fanning, Washington, and Palmyra) are rarely visited by ornithologists, we thought it worthwhile to report our observations.

The author is indebted to Dr. Frank Richardson for his helpful review of the manuscript.

Christmas Island (Fig. 1), lies in the equatorial Pacific about 1,200 miles south of Hawaii at 2° N. latitude, 157° W. longitude. It is about 35 miles in length, in a northwest–southeast direction, and about 17 miles in width. The island is a large coral atoll with a perimeter of about 105 miles. Enclosed within the outer coast is an area estimated at 382 square miles, of which approximately 250 are land and 107 are lagoon; about 25 square miles are occupied by numerous salt lakes (Wentworth, 1931). The island is generally low, averaging about 10 feet or less in elevation, except along the southern shore of the Bay of Wrecks where there are scattered sand dunes which may reach 40 feet in height.

The rainfall is quite variable but averages 25 to 35 inches a year (Bryan, 1942). Fragmentary records show an annual range from 10 inches to as much as 100 inches. The air temperature varies from a minimum of 68° or 70° F. to a maximum of 106° F. (Wentworth, 1931).

Christophersen (1927) records 24 species of vascular plants as growing naturally on Christmas Island. These include *Tournefortia argentea* trees, clumps of *Scaevola frutescens* and other low shrubs, grasses, and herbs. Although all the coconut palms now seen on the island have been planted, there were a few palm trees present at the time of Captain Cook's visit in 1777. There are now extensive coconut groves in the northwestern, northern, southwestern, and southern parts of the island.

The vertebrate fauna of the island consists mainly of the fishes that abound in the lagoon and coastal waters and the abundant bird life that forms the subject of this report. In addition there are lizards, rats, and cats; many of the latter roam in a wild state, and while they may help keep down the rat population, they also without doubt prey on the ground-nesting birds.

Great Britain claims sovereignty over the island and has brought in natives from the Gilbert and Ellice Colony to provide a labor

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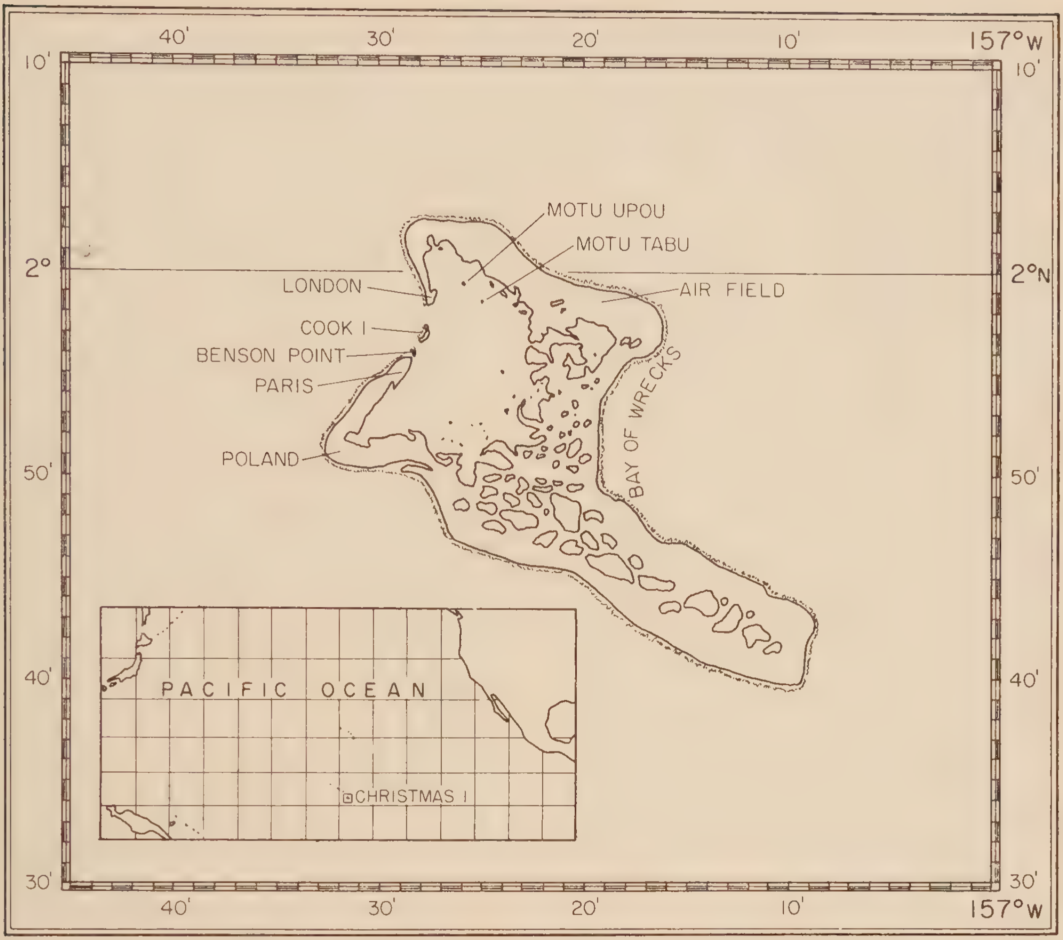

FIG. 1. Christmas Island, showing locations referred to in the text and the island's general position in the central Pacific (inset). (Drawn with modifications from USN Hydrographic Office Chart No. 1839.)

force for the plantation. There is no indigenous population.

A review of the literature describing the avifauna of Christmas Island begins with the account of its discoverer, Captain James Cook. On the afternoon of December 24, 1777, Captain Cook brought his ships the "Resolution" and the "Discovery" to anchor off the west shore of the island. On the next day—Christmas Day—he and his men went ashore at Cook Island (Fig. 1), a small patch of coral and sand separated from the main island. He states (Cook, 1784), "As we kept our Christmas here, I call this discovery Christmas Island." The vessels stayed at anchor several days to permit the men to refresh themselves and to observe an eclipse of the sun. Cook reports that there were no traces of human beings having been there before and that the number of coconut trees did not exceed 30. He had the following to say about the animal life *ibid.*, p. 188–189):

> Under the low trees above-mentioned, sat infinite numbers of a new species of tern, or egg-bird. These are black above, and white below, and with a white arch in the forehead [apparently sooty terns]; and are rather larger than the common noddy. Most of them had lately hatched their young, which lay under old ones, upon the bare ground. The rest had eggs; of which they only lay one, larger than that of a pigeon,

bluish and speckled with black. There was also a good many common boobies; a sort that are almost like a gannet [most likely the blue-faced booby]; and a sooty or chocolate-coloured one, with a white belly [the brown booby]. To this list we must add men-of-war birds; tropic-birds; curlews; sand-pipers; a small land-bird like a hedge sparrow [the kokikokiko, as named by the Gilbertese]; land crabs; small lizards; and rats.

The whaling ship "Tuscan" stopped at Christmas Island in May, 1835. Bennett (1840) gives an interesting account of the visit and states that, "Here and there among the low thicket scrubs are vast rookeries of aquatic birds, whose clamour is deafening." He mentions "sooty terns," "red-tailed tropic birds," "pure snow white petrels," probably white terns, "boobies," blue-faced boobies from the description, other "terns," probably noddies, "frigate birds," "petrels," "curlews," bristle-thighed curlews, "quail," probably golden plover, and a "sparrow-like land bird," the kokikokiko.

Streets (1877) visited Christmas Island in the vessel "Portsmouth" during the course of the United States North Pacific Surveying Expedition of 1873–75. Nine species of birds were reported and a collection was made. Father Emmanuel Rougier (1914), who at one time held a lease on the island, has published one of the most complete descriptions of Christmas Island, including its flora and fauna. He lists the following birds: frigate bird, sooty tern, grey-backed tern, Necker Island tern, Hawaiian tern, noddy tern, white tern, Christmas Island shearwater, red-tailed tropic bird, blue-faced booby, red-footed booby, and the kokikokiko (a small land bird), a total of 12 species. Kirby (1925) reports 11 species of sea and shore birds (including the bristle-thighed curlew, wandering tattler, and golden plover) plus several kinds of migratory ducks (which he does not name) as occurring on the island. He states that birds have been greatly reduced in number (prior to 1925) throughout the Line Islands as a result of land clearing and other disturbances by man. In 1921 the Whitney Expedition of the American Museum of Natural History carried on an investigation of the birds of Christmas Island. Specimens of the kokikokiko, *Conopoderas aequinoctialis aequinoctialis* (Latham), collected at this time have been described by Murphy and Mathews (1929).

The following is a list, with a few life-history notes, of the birds seen by the author during his stay on Christmas Island from October 23 to December 9, 1953. In general, Peters (1931, 1934) has been followed in respect to scientific names.

Puffinus nativitatus Streets, Christmas Shearwater. Abundant. Observed nesting with eggs and young on the islets of Motu Tabu and Motu Upou within the lagoon. Nests were in shallow tunnels or depressions over-hung with grass or low shrubs.

Pterodroma alba (Gmelin), Phoenix Petrel. Abundant. Observed nesting with eggs (Fig. 2*d*) and young on the islets of Motu Tabu and Motu Upou. This petrel could be seen throughout the day, flying low over the land and lagoon, and was more commonly seen over land than was the Christmas shearwater. Nesting habits were the same as for that species.

Nesofregetta albigularis (Finsch), White-throated Storm Petrel. Uncommon. Observed near shore (October 22) when we were approaching the island from the north, and seen on several occasions flying over the lagoon and outer beach. One bird of this species was found nesting, with one egg, on the islet of Motu Tabu. The egg was in a shallow depression over-hung by a thick cover of grass.

Phaethon rubricauda melanorhynchos Gmelin, Red-tailed Tropic Bird. Abundant. Observed nesting with eggs and young (Fig. 2*c*) throughout the island. Egg usually was placed under the low shrubs of *Scaevola* or the larger *Tournefortia*.

Sula sula rubripes Gould, Red-footed Booby. Abundant and generally distributed throughout the island. Nests with eggs and young (Fig. 2*e*) were observed principally in *Tournefortia* trees.

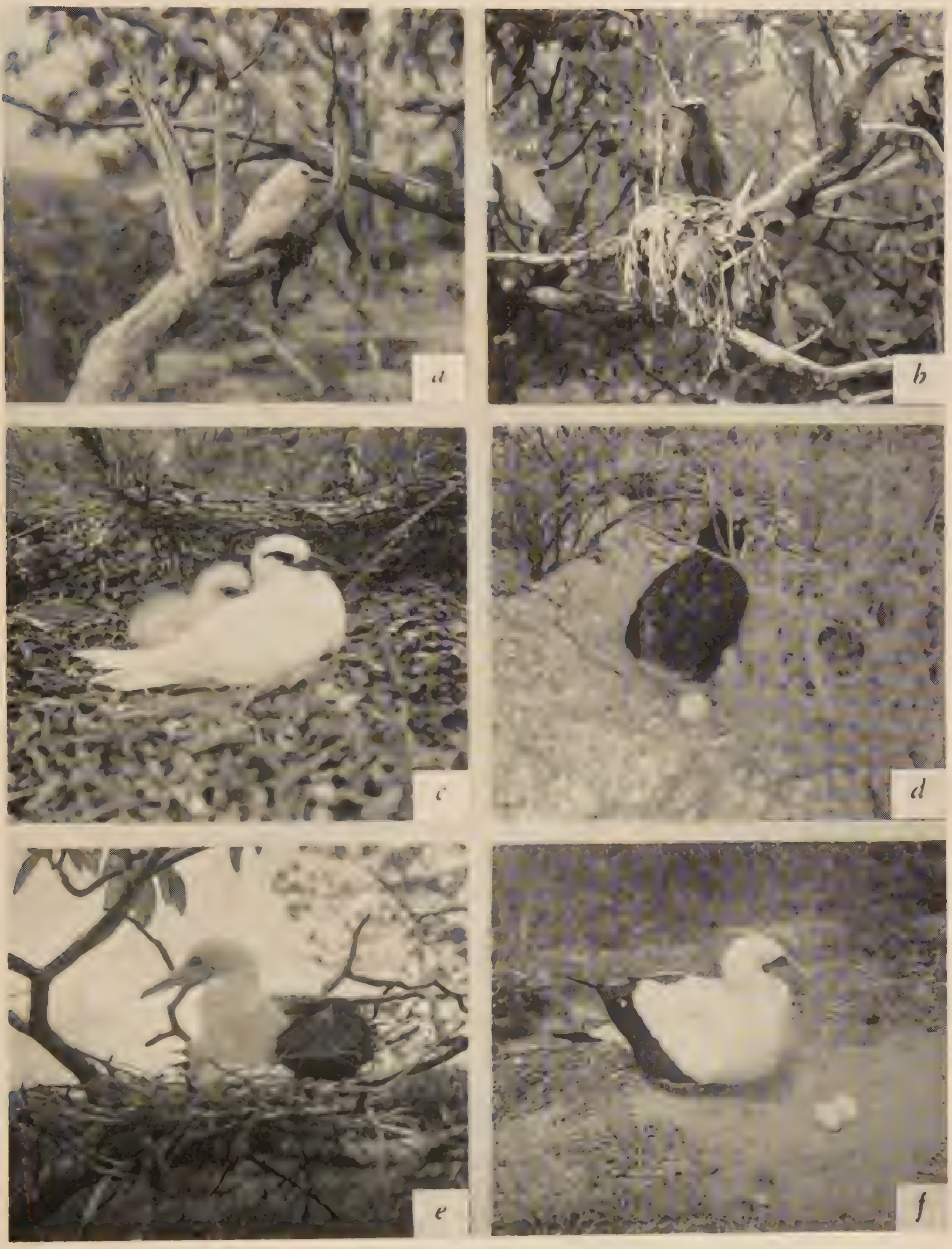

FIG. 2. Some of the birds of Christmas Island; photographed by the author. *a*, Young white tern on the remains of a nest of the white-capped noddy; *b*, young white-capped noddy on the nest; *c*, red-tailed tropic bird with young; *d*, Phoenix petrel with egg; *e*, red-footed booby with young; *f*, blue-faced booby with eggs.

Sula dactylatra personata Gould, Blue-faced Booby. Common but considerably less so than *S. s. rubripes*. Eggs and young were observed principally in the less visited areas. The eggs are deposited on the ground in a slight depression with no nesting materials (Fig. 2*f*). A booby of this species was seen setting on two eggs on October 28, one of which hatched on December 8 indicating that the incubation period exceeds 42 days.

Sula leucogaster plotus Forster, Brown Boody. Common in certain areas, such as the Bay of Wrecks and Benson Point. No eggs or young were seen.

Fregata minor palmerstoni Gmelin, Frigate Bird. Abundant, but not observed to be nesting. These birds seemed to make their living primarily at the expense of the boobies, which they would attack by diving from a considerable height and continually torment until the unfortunate booby surrendered its food. Specimens in immature plumage were common.

Sterna fuscata oahuensis Bloxham, Sooty Tern. The most abundant bird on the island. Was present in large numbers in October but appeared in huge congregations in the latter part of November and started to nest in the first week of December. The main nesting areas were located in the northwestern part of the island, between Poland and Paris, on Cook Island, and on parts of the large southeastern peninsula.

Thalasseus bergii cristatus Stephens, Crested Tern. Common; not observed to be nesting. This is the largest tern of the Pacific and not previously reported for Christmas Island.

Anous stolidus pileatus (Scopoli), Common Noddy. Common but found with eggs only on Cook Island during our visit. Eggs were deposited on the ground under *Scaevola* shrubs.

Procelsterna cerulea cerulea (F. D. Bennett), Blue-grey Noddy. Abundant. Observed with eggs and young on Cook Island and Motu Tabu. The eggs were found in areas almost barren of vegetation.

Anous minutus minutus Boie, White-capped Noddy. Common. Was nesting with eggs and young on Cook Island, Motu Tabu and Motu Upou (Fig. 2*b*). The nest was constructed of leaves, twigs, and grass and placed in the *Tournefortia* trees.

Gygis alba candida (Gmelin), White Tern. Abundant. Observed with eggs and young (Fig. 2*a*) on Cook Island, Motu Tabu, and Motu Upou. The egg is deposited on a bare horizontal trunk or limb of the larger shrubs or trees. The eggs are easily dislodged and the writer returned many eggs, which had fallen to the ground, to their former location after flushing the incubating adult bird. These terns were observed returning to their young with what appeared to be four to six small fish lined up in their beaks. This feat has been noted many times and while it is thought that the tongue may assist in the operation, the details of the phenomenon still remain a mystery.

Anas acuta tzitzihoa Vieillot, Pintail Duck. One or two ducks of this species were occasionally sighted in the ponds near the airfield. From the shore of the Bay of Wrecks, on November 18, a flock of about 20 birds thought to be pintails, were seen flying in off the ocean from the northeast.

Pluvialis dominica fulva (Gmelin), Pacific Golden Plover. Abundant. Occurring generally throughout the island even in the streets of the native village. In fact it seemed more abundant in the dry areas with little vegetation than along the beaches and mud flats. During the period of our visit birds were seen in a variety of plumage patterns from the dark-breasted breeding plumage to the light-breasted winter condition.

Numenius tahitiensis (Gmelin), Bristle-thighed Curlew. Common to abundant. Observed in many different habitats on the island, from the dry interior areas to the ocean and lagoon beaches.

Heteroscelus icanus (Gmelin), Wandering Tattler. Probably the most abundant shore bird on the island, occurring almost everywhere near water.

Arenaria interpres interpres (Linnaeus), Turnstone. Small flocks of these birds were seen on three occasions at the ponds near the airport.

Crocethia alba Pallos, Sanderling. One bird of this species was seen near London Village on the morning of November 7.

Larus delawarensis Ord, Ring-billed Gull. An immature specimen of this species was sighted in the lagoon behind London Village on November 15. It was examined at close range twice that day and again the next two days, but not seen thereafter. This bird is certainly a rare visitor to the central Pacific and the author is not aware of any previous record of the species for the Line Island group.

Conopoderas aequinoctialis aequinoctialis (Latham), Kokikokiko. Common in the higher and more dense growths of *Tournefortia*. Old nests were found but none containing eggs or young. This species is flycatcher-like in appearance and is the only native land bird on the island. These birds stayed close to cover and were rarely seen in flight.

Although the author was in the field every day during the 7-week stay and covered the island rather thoroughly several times, except for the long peninsula extending to the southeast, it is very probable that the above list is not complete for the period of our visit. For example, the wedge-tailed shearwater (*Puffinus pacificus chlororhynchus* Lesson), one of the most abundant of the Procellariidae in the mid-Pacific, is reported to nest on the island (Alexander, 1928; Murphy, 1951) but was not seen there during our visit. The gray-back tern (*Sterna lunata* Peale) is supposed to occur throughout Oceania (Alexander, 1928) and has been observed on Christmas Island (Rougier, 1914). We believe we sighted this bird on a few occasions but were not able to identify it with certainty. The white-tailed tropic bird (*Phaethon lepturus dorotheae* Mathews) has been observed by the author on Fanning and Washington islands but not on Christmas, and according to Kirby (1925) it does not occur there. The author has also admired the brightly colored parakeets, *Vini kuhlii* (Vigors), on Fanning and Washington islands but did not find them on Christmas and probably they have never become established there (Tristram, 1883). The black-footed albatross (*Diomedea nigripes* Audubon) is common in the temperate and subtropical North Pacific and has been observed by the author as far south as 7° N. latitude (on December 14, 1953). It may occasionally visit the Line Islands area, but as yet we have not encountered it there on any of the several POFI cruises from 1950 to 1954.

Except for the golden plover, tattler, and curlew, there was a general lack of shore birds on the island during the period of our stay. Ducks also were scarce. About the middle of November, Mr. Phil Palmer of Fanning Island, which is about 150 miles northwest of Christmas, reported that a large number of ducks had just arrived on that island during a rainstorm. Apparently none of these birds reached Christmas.

Some information of interest and value was obtained from Latia, the "old man" of the island. He reported that on Christmas Island the sooty terns have two nesting periods: a mid-winter period from December to March, and a mid-summer period from June to August. About equal numbers of birds take part in each nesting. The red-tailed tropic birds nest from June to January and the frigate birds from December to June. There are some shearwaters and petrels nesting throughout the year. The boobies have eggs and young over a good part of the year, particularly during the fall and winter months. Usually a few ducks show up each winter but never in great numbers. Mr. Richard Cooper, British Officer for the Line Islands, reported that the small land bird, called the "kokikokiko" by the Gilbertese, lays its eggs in the summer months.

In summary, 22 species of birds were identified on Christmas Island during the period October 23–December 9, 1953. Of this number, 11 species were observed with eggs or with eggs and young. The author believes this to be the first report of the occurrence of the crested tern and the ring-billed gull on Christmas Island or for the Line Island area.

ADDENDUM

Since the submission of this manuscript the author has made another visit to Christmas Island, June 5 and 6, 1954. Other duties prevented a thorough survey of the Island, but through the courtesy of British District Officer Percival Roberts, a short trip was made to the islet of Motu Tabu. Species observed nesting with eggs and young were the Christmas shearwater, white-capped noddy, common noddy, white tern, and red-tailed tropic bird. The Phoenix petrel was brooding eggs, but no young were seen. The blue-grey noddy was quite abundant on the islet, but no eggs or young could be found. Sooty terns, crested terns, frigate birds, and red-footed boobies were observed flying over the lagoon. Some of the Gilbertese plantation staff informed us that the sooty terns had not yet started to nest but had already begun to congregate on the main island for their summer nesting season.

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VARIATIONS IN ZOOPLANKTON ABUNDANCE IN THE CENTRAL EQUATORIAL PACIFIC, 1950-1952

DIOCESAN PRESS, MADRAS

VARIATIONS IN ZOOPLANKTON ABUNDANCE IN THE CENTRAL EQUATORIAL PACIFIC, 1950-1952

by

J. E. King*

The abundance of zooplankton as an index to potential fish production is significant to the study of the high seas fishery resources of the tropical and sub-tropical regions of the central Pacific being carried out by the Pacific Oceanic Fishery Investigations (POFI) of the U.S. Fish and Wildlife Service. In this report we shall review the primary results of our zooplankton sampling in the equatorial Pacific from our initial year, 1950, through 1952. The data will be examined for variations associated with latitude, longitude, and season. We shall point out, very briefly, certain relationships which appear to exist among the hydrographic features of the environment, the zooplankton, and the tunas.

Zooplankton is a basic food of much of the vertebrate fauna of the sea. It is directly utilized even by such large and fast moving fish as the tunas, the group of fish presently under study by these Investigations. For example, representatives of the following groups have been captured in our plankton nets and have also been found among the stomach contents of maturing and adult yellowfin tuna (Reintjes and King, 1953).

mysids
euphausiids
amphipods
stomatopod larvae
shrimps
palinurid larvae
brachyuran larvae
heteropods
pteropods
cephalopods
tunicates
fish larvae and juveniles

The bulk of the zooplankton, however, reaches the tunas indirectly through intermediary forage organisms such as squid, fish, and the larger shrimp.

Earlier plankton sampling in this area has consisted principally of scattered collections. Some of the major oceanographic expeditions, the *Challenger* the *Albatross* and the *Dana*, while traversing the central Pacific, made a few hauls which were largely qualitative and chiefly of value in systematic and distributional studies. The *Carnegie* visited the central Pacific in 1929 and made quantitative hauls on a generally north-south section crossing the Equator. The resulting data (Graham, 1941) are difficult to compare with our own but do provide evidence on variation in plankton dry weights as related to latitude and the equatorial current system. The work being carried out by POFI is, however, the first comprehensive quantitative survey of zooplankton abundance in the equatorial central Pacific and the first attempt to correlate the physical and chemical environment, zooplankton abundance, and tuna catch.

The Pacific Oceanic Fishery Investigations are under the directorship of Mr. O. E. Sette, who has contributed many of the ideas expressed in this report. Miss Joan Demond[1] and Mr. Thomas S. Hida[2] assisted in making the zooplankton volume determinations on which this report is based. We are indebted to Messrs. Garth I. Murphy[3] and Richard S. Shomura[3] for supplying the yellowfin tuna catch records. The hydrographic data were collected and processed under the supervision of Messrs. Thomas S. Austin[4] and Townsend Cromwell[5]. The author is responsible for combining and averaging the tuna catch records and the inorganic phosphate data for the purpose of comparing them with the zooplankton volumes.

This report is based on 405 collections taken on 10 cruises of the Fish and Wildlife Service vessel *Hugh M. Smith* during the years 1950 to 1952. The time of year of each cruise, the general area visited and the number of collections are listed in Table 1. The area sampled (Fig. 1) extends from 120° W. longitude on the east to 180° longitude on the west, with a range of latitude from 27° N. (on 175°W. longitude, to 14-1/2° S. (on 172°W. longitude). The geographic position for each plankton station and the value of each collection as a count or volume of zooplankton have appeared, or will appear, in other publications of the Fish and Wildlife Service (King and Demond, 1953; King and Hida, 1954). Most of the cruises consisted of one or more long series of stations (as illustrated in Fig. 2 for cruise 5) extending in a north-south direction, crossing the Equator and the major equatorial currents.

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Cruises 2, 5, 8, 15 and 16 were combined hydrographic and plankton cruises and thus provide information on currents, temperatures, oxygen and inorganic phosphate for comparison with the zooplankton abundance. Cruises 7, 9 and 18 of the *Smith* were primarily tuna fishing expeditions on which some plankton collections were made; cruises 11 and 14 were combination fishing, hydrographic and plankton cruises.

The plankton nets used in making these collections were 1 meter in mouth diameter and about 5 meters in overall length. Front and middle sections of the net were of 30xxx silk grit gauze (apertures 0.65 mm square); the rear section and bag were of 56xxx grit gauze (apertures 0.31 mm square). The 30xxx grit gauze comprised about 97 per cent of the straining surface of the net.

Nets of this mesh size retained the tuna eggs (of about 0.80 mm diameter) and tuna larvae, the capture of which was one object of the study. Almost all phytoplankton passed through the net, and thus a relatively "clean" sample of zooplankton was obtained. A flow meter suspended in the mouth of the net gave an estimate of the amount of water strained on each haul. Thus the results could be expressed in terms of cubic centimeters of zooplankton per unit of water strained.

As we were limited to a single tow at each station, we chose to use, for the greater part, an oblique haul. This method of hauling has been shown by Winsor and Clarke (1940) to be subject to less sampling error and to provide more reliable and consistent results than vertical or horizontal hauls. In making the haul the net was lowered at a slow, uniform speed to a calculated depth of 200 meters (estimated from wire out and angle of stray from the vertical, assuming the towing wire to describe a straight line in the water), and then retrieved at the same slow, uniform speed. Following this practice the oblique tow to 200 metres required about 30 minutes, and approximately equal amounts of time were spent at all depths. The amount of water strained on each haul varied from 1,000 to 1,500 cubic metres.

For cruises 2, 5, 7 and 8, a measured fraction of each sample was counted and the displacement volume was determined (the zooplankton counts are not utilized in this report). For all subsequent cruises, the displacement volume of the entire sample was measured but no counts were made. During the course of the work, refinements in technique have been introduced which tend to give a more accurate estimate of the amount of zooplankton—as food—present at each station. Detailed descriptions of the methods employed in processing the samples are given in recent reports (King and Demond, 1953; King and Hida, 1954).

For purposes of comparison, the zooplankton volumes were grouped according to their position into 5-degree intervals of latitude and 10-degree intervals of longitude. The intervals of latitude chosen were as follows: 0°00′ to 4°59′, 5°00′ to 9°59′, etc. The few samples occurring at 0°00′ were assigned to the 0°-4°N. group or the 0°-4° S. group depending upon the direction the section was being traversed, e. g., if the direction of movement was to the south, the sample was assigned to the southern (0°-4° S.) group. The intervals of longitude selected were as follows: 120° to include samples from 115°00′ to 124°59′, 130° to include samples from 125°00′ to 134°59′, etc.

When the data from all 10 cruises were combined irrespective of longitude and season into 5-degree latitudinal groups and graphically portrayed as in figure 3B, the peak of abundance was found to occur near the Equator in the South Equatorial Current but displaced slightly to the northward and spilling over somewhat into the Countercurrent. The poorest areas within the range of latitude sampled were those in the North Equatorial Current. An average of zooplankton volumes, included in figure 3B, obtained on four cruises in Hawaiian waters during the years 1951 to 1953 shows that Hawaii ranked a little higher than parts of the North Equatorial Current, but considerably lower than the equatorial region.

Figure 3B is a composite, however, including many cruises occurring at different times of the year and with sampling along different longitudes, from 120° W. to 180°. A more accurate picture may be obtained from Table 2, where the latitudinal variation is shown for each 10 degrees of longitude. Table 3 is included to point out differences among four major cruises, with two cruises (2 and 8) occurring during the northern winter season and two cruises (5 and 11) occurring in the late northern summer. Through an analysis of variance, King and Demond (1953) found no significant differences ($P > 0.05$) between longitudes for both cruises 5 and 8 but highly significant differences ($P < 0.01$) between cruises. In general, it appears that the equatorial region produced a larger zooplankton crop in the winter of 1950 than in the winter of

1951. The summer crops of the two years are about equal.

Table 4 was constructed for the purpose of examining further the variations with season of the year and with longitude. The sampled area included portions of both hemispheres and since we as yet had no evidence as to natural seasons in zooplankton abundance in the tropical Pacific, the calendar year was divided into quarters as indicated in Table 4. Since latitude is a third variable to be taken into account, Table 4 is arranged to show variations with longitude and "season" for three latitudinal groups: 4°N-0°, 0°-4°S, and 9° N-4° S. These are the latitudes for which we have the most observations and they are also the areas of greatest plankton production. The border means in the table indicate that longitudes 160° to 120° produced in general the largest volumes, although our data are not sufficiently complete to provide entirely reliable conclusions. Figure 4A, which summarizes the variation with longitude for all observations between 9° 59′ N. and 4° 59′ S. latitude, shows a gradient of increasing abundance from west to east, with a levelling-off east of 140°. Certain of the longitudes were sampled at only one period of the year, however, so this picture of longitudinal variation may change somewhat with future sampling.

In respect to seasonal variation, the period January—February—March ranked low for most longitudes. July—August—September, almost without exception, marked the period of greatest production (great significance should probably not be attributed to the three observations for October — November — December, 4°N.-0° latitude, 160° W. longitude). Perhaps the most striking feature of the data as portrayed in Figure 4B is the absence of the great seasonal variation which is so characteristic of plankton abundance in higher latitudes.

Tropical seas have been considered less productive than those of higher latitudes on the grounds that surface heating in the tropics results in a stable stratification of the sea, thus limiting vertical mixing by convection which would bring nutrients to the euphotic zone (Delsman, 1939, Graham, 1941; Sverdrup *et al.*, 1942, p. 942). Such thermal stratification does apparently exist throughout much of the tropical and sub-tropical Pacific. It was learned, however, from the last cruise of the *Carnegie* in 1929, that these generally stable conditions are disrupted at the Equator by a divergence of the surface waters resulting in upwelling. The latter was considered responsible for enrichment of the surface waters and the production of much greater concentrations of plankton than were found in higher latitudes within the tropics and sub-tropics (Graham, 1941).

The existence of the divergence at or near the Equator, with resultant upwelling of nutrient-rich water, is substantiated by the researches of this laboratory. The nature of the upwelling and the causal forces involved are discussed by Cromwell (1951 and 1953) and Sette (MS). Apparently the strong east and southeast trade winds which prevail for the greater part of the year and the effect of the Coriolis force are the major influences governing this equatorial current system.

Basic nutrients, brought to the surface by the equatorial upwelling, are essential to the growth of phytoplankton; in the present studies the concentration of dissolved inorganic phosphate is used as an indicator of these nutrients. Figure 3A shows the variation in inorganic phosphate with latitude, as found on seven cruises in the central Pacific. We have no empirical explanation at the present time for the asymmetric distribution of phosphate with respect to the Equator. This may be related, however, to differences in the meridional components of the surface current in the region of the Equator, or perhaps to differences in the rate of utilization by phytoplankton. As indicative of the phosphate ⟶ phytoplankton ⟶ zooplankton eutrophic linkage, we have found a highly significant positive correlation between zooplankton and inorganic phosphate on the long north-south sections crossing the Equator (King and Demond, 1953).

The frequently appearing "fronts" (Cromwell, 1953) in the zone of convergence north of the Equator, at 2° to 4° N. latitude, may also contribute to the apparent greater abundance of life in the equatorial region. Floating organisms of high buoyancy may tend to congregate along the fronts just as driftwood does along a "current rip." Motile plankton forms capable of resisting the downward currents would also tend to concentrate in the surface waters; thus a rich pasturage for plankton-feeding animals could result.

The unusual abundance of marine life in the region of the Equator and the Countercurrent has been observed by many expeditions and world travellers while crossing the Pacific. The surface manifestations of the enrichment may have a counterpart in certain features of the bottom deposits of this area of the Pacific. Revelle (1944) points out the agreement between the southern boundary of the Countercurrent and the northern border of the Pacific *Globigerina* ooze area. Arrhenius

(1950) concluded from an examination of bottom samples collected by the Swedish Deep-Sea Expedition that in the Pacific the " biogenous component " increases strongly in the region between the Equator and the southern boundary of the Countercurrent "—where a biolith, rich in fossils of foraminifera, radiolaria and diatoms is thus deposited."

From October, 1950, to June, 1953, the Pacific Oceanic Fishery Investigations conducted experimental longline fishing for tuna on 10 cruises in waters of the equatorial Pacific. The fishing took place in essentially the same area with about the same boundaries of latitude and longitude as our plankton investigations. The longline method of fishing and the results obtained on these cruises have been reviewed by Murphy and Shomura (1953*a* and 1953*b*).

In the Pacific, several species of tuna are taken by the longline fishing method. In the equatorial central Pacific the yellowfin, *Neothunnus macropterus* (Temminck and Schlegel), constitutes by far the largest percentage of the catch. When the catches, in terms of yellowfin captured per hundred hooks fished at each station, are combined in 5-degree intervals of latitude, irrespective of longitude and time of sampling—as was done for the zooplankton to produce Figure 3B — the result (Fig. 3C) indicates the area of best catch to be at 4°N.—0° latitude. The average catch rate drops off very fast to the north and south of these latitudes.

It is rather obvious that there is more than a casual relationship between zooplankton and yellowfin tuna, but, as might be expected when using the average values of zooplankton and fish from a number of disconnected cruises, the latitudinal distribution of zooplankton and fish do not precisely correspond. There are several reasons why this might be so, but for the present discussion it is enough to establish that one of the basic food constituents of tuna — plankton — reaches a peak of abundance near the Equator in a region high in mineral nutrients and that this same region is also found to contain maximal concentrations of yellowfin tuna.

In summary it would seem that upwelling at the Equator, resulting from the equatorial divergence, replenishes the supply of nutrients in the surface waters and provides a suitable environment for the growth of phytoplankton. Since animal life depends on its food supply, conditions in this region are favourable for the development of a zooplankton population. Convergence in the surface water layers, occurring usually at 2° to 4° N. latitude, between the Equator and the southern boundary of the Countercurrent, tends to concentrate the zooplankton into a rich pasturage for forage organisms. These in turn serve as food for the larger fishes such as the tunas. Thus, a productive cycle in the sea, starting from upwelled equatorial waters, results in the formation of a vast potential food resource in the form of yellowfin tuna.

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Table 1

Cruise period, general area visited, and number of zooplankton samples collected on 10 cruises of the U.S. Fish and Wildlife Service vessel *Hugh M. Smith* during the years 1950 to 1952.

Cruise	Cruise period	Approximate longitude	Range of latitude	Number of samples
2	Jan.-Feb. 1950	170°W	23°N-4°S	12
	Feb.-Mar. 1950	160°W	19°N-4°S	12
5	June 1950	180°	27°N	1
	July 1950	170°W	25°N-5°S	26
	July-Aug. 1950	160°W	20°N-4°S	24
7	Oct.-Nov. 1950	160°W	20°N-2°N	23
	Nov. 1950	170°W	6°N	1
8	Jan. 1951	150°W	6°N	1
	Jan.-Feb. 1951	160°W	20°N-7°S	41
	Feb.-May 1951	170°W	20°N-14°S	45
9	June 1951	180°	25°N	1
	June 1951	170°W	22°N-4°S	13
	June 1951	160°W	20°N-1°S	11
11	Sept. 1951	150°W	19°N-4°S	45
	Sept. 1951	160°W	2°N-1°N	5
14	Jan.-Feb. 1952	150°W	7°N-3°S	7
	Jan.-Feb. 1952	160°W	1°N-6°S	9
	Mar. 1952	170°W	6°N-5°S	13
	Mar. 1952	180°	9°N-8°S	18
15	May-June 1952	140°W	9°N-7°S	60
16	Aug. 1952	150°W	2°N-3°S	14
18	Oct. 1952	120°W	7°N-8°S	13
	Nov. 1952	130°W	9°N-4°S	10

Table 2

Variation in zooplankton abundance as associated with latitude and longitude without regard to time of year of sampling. Figures given are means of zooplankton volumes (as cc per 1000m^3 of water strained). [Number of samples for each area ncluded in parentheses.]

	180°	170°	160°	150°	140°	130°	120°	Mean
29°-25°N	12.5(2)	27.1(1)	..	..	..	..	..	17.4(3)
24°-20°	..	16.5(6)	24.6(4)	..	..	..	..	19.8(10)
19°-15°	..	21.6(8)	31.7(10)	16.4(3)	..	..	..	25.7(21)
14°-10°	..	14.7(13)	22.0(21)	20.1(8)	..	..	..	19.4(42)
9°-5°	19.6(5)	23.8(19)	30.6(31)	26.8(13)	51.2(18)	37.3(3)	41.8(2)	32.6(91)
4°-0°	27.2(5)	37.0(24)	37.0(34)	37.7(28)	34.8(17)	35.8(4)	38.2(6)	36.5(118)
0°-4°	25.9(4)	32.6(28)	36.8(20)	39.9(15)	38.9(19)	34.2(3)	37.9(3)	35.9(92)
5°-9°	15.4(4)	20.8(8)	28.7(5)	..	21.8(6)	..	29.6(2)	22.5(25)
10°-14°S	..	16.5(3)	..	..	..	..	..	16.5(3)
Mean*	24.1(14)	31.7(71)	34.6(85)	35.8(56)	41.7(54)	35.8(10)	38.8(11)	

* For latitudes 9°N to 4°S only.

Table 3.

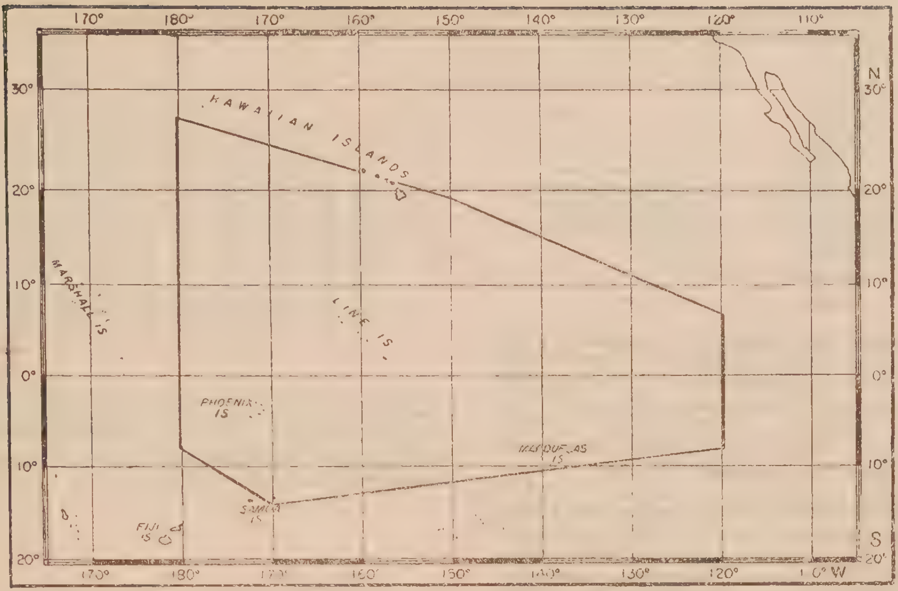
Variation in zooplankton abundance with latitude as obtained on four major cruises of the *Hugh M. Smith.* Valu given are mean zooplankton volumes (as cc per 1000m^3 of water strained). [Number of samples for each area include in parentheses].

Latitude	Cruise 2		Cruise 5		Cruise 8		Cruise 11	
	Feb. 1950		July 1950		Feb.-Mar. 1951		Sept. 1951	
	170°	160°	170°	160°	170°	160°	150° Section 1	150° Section 2
24°-20°N	10.8(2)	..	21.4(2)	28.9(1)	14.5(1)	15.4(1)	..	..
19°-15°	..	17.6(1)	25.9(3)	28.6(2)	14.2(3)	10.5(1)	..	16.4(3
14°-10°	11.2(3)	6.6(3)	20.4(4)	23.3(6)	12.5(5)	19.7(5)	17.0(3)	22.0(5
9°-5°	23.1(2)	26.4(3)	25.4(6)	43.2(5)	21.0(6)	23.4(12)	24.4(5)	31.0(4
4°-0°	53.2(2)	74.0(2)	42.0(4)	62.2(4)	35.4(12)	24.7(15)	41.6(10)	45.0(6
0°-4°	53.7(3)	57.7(3)	53.8(5)	36.5(6)	21.4(8)	36.8(4)	45.6(5)	58.6(4
5°-9°	..	..	31.5(1)	..	19.3(7)	34.1(3)	..	..
10°-14°S	..	..	..	..	16.5(3)	..	..	..

Table 4.

Variation in zooplankton abundance with longitude and time of year of sampling for certain latitudinal zones. Valu are mean zooplankton volumes (as cc per 1000m^3 of water strained). [Number of samples for each area and season enclos in parentheses].

	Jan.-Feb.-Mar.	Apr.-May-June	July-Aug.-Sept.	Oct.-Nov.-Dec.	Mea
4°N-0°					
180°	27.2(5)	..	..	..	27.2
170° W	36.8(19)	20.1(1)	42.0(4)	..	37.0
160°	29.2(19)	27.7(3)	46.4(9)	68.0(3)	37.0
150°	25.0(3)	..	39.3(25)	..	37.7
140°	..	34.8(17)	..	..	34.8
130°	..	..	..	35.8(4)	35.8
120°	..	..	..	38.2(6)	38.2
Mean	31.8	33.1	41.2	44.3	
0°-4°S					
180°	25.9(4)	..	..	..	25.9
170° W	27.5(17)	29.2(6)	53.8(5)	..	32.6
160°	38.5(12)	27.6(2)	36.5(6)	..	36.8
150°	26.3(1)	..	40.9(14)	..	39.9
140°	..	38.9(19)	..	..	38.9
130°	..	..	..	34.2(3)	34.2
120°	..	..	..	37.9(3)	37.9
Mean	31.2	35.9	42.4	36.1	
9°N-4°S					
180°	24.1(14)	..	..	..	24.1
170° W	30.2(46)	27.8(9)	39.3(15)	19.2(1)	31.7
160°	29.9(46)	28.7(7)	42.6(20)	42.8(12)	34.6
150°	25.4(8)	..	37.5(48)	..	35.8
140°	..	41.7(54)	..	..	41.7
130°	..	..	..	35.8(10)	35.8
120°	..	..	..	38.8(11)	38.8
Mean	29.0	38.6	39.1	38.7	


170°
180°
170°
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130°
120°
110°
N
30°
20°
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0°
S
110° W
HAWAIIAN ISLANDS
MARSHALL IS
LINE IS
PHOENIX IS
MARQUESAS IS
SAMOA IS
FIJI IS

FIG. 1.—Map of the central Pacific showing the boundaries of the area covered in these investigations.

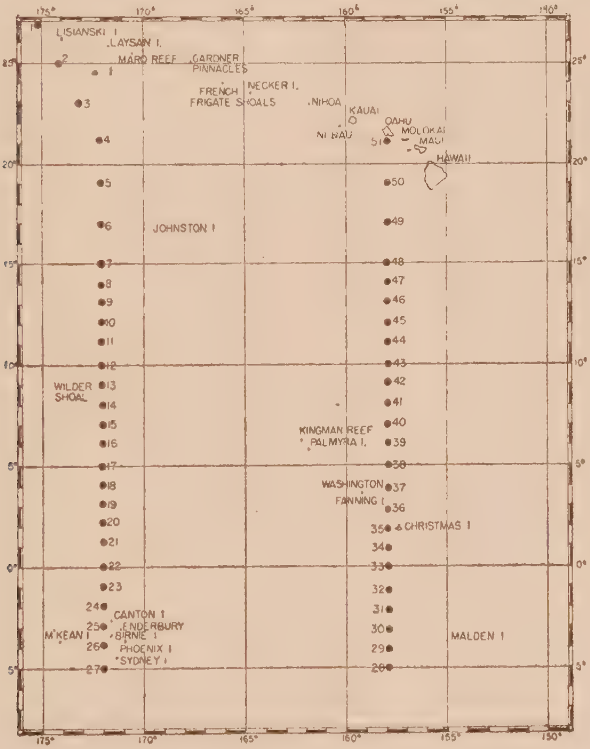
175°
170°
165°
160°
155°
150°
25°
20°
15°
10°
5°
0°
LISIANSKI I
LAYSAN I.
MARO REEF
GARDNER PINNACLES
NECKER I.
FRENCH FRIGATE SHOALS
NIHOA
KAUAI
NIIHAU
OAHU
MOLOKAI
MAUI
HAWAII
JOHNSTON I
WILDER SHOAL
KINGMAN REEF
PALMYRA I.
WASHINGTON
FANNING I
CHRISTMAS I
CANTON I
ENDERBURY
BIRNIE I
M'KEAN I
PHOENIX I
SYDNEY I
MALDEN I

FIG. 2.—Plankton station positions for cruise 5 of the *Hugh M. Smith*, showing the station pattern of one of the combined hydrographic and plankton cruises.

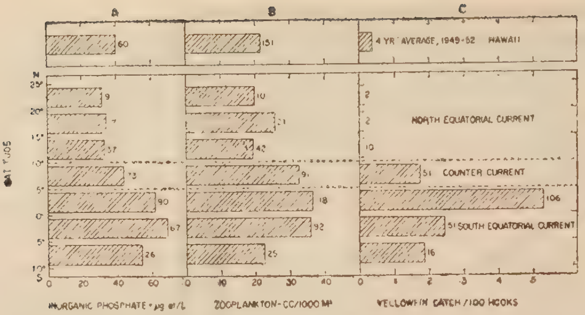

FIG. 3.—Variation with latitude of inorganic phosphate (A), zooplankton abundance (B), and yellowfin tuna catch (C), with the data combined into 5-degree intervals of latitude without regard to longitude and time of year. The approximate boundaries of the major equatorial currents are indicated. Part A is derived from cruises 2, 5, 8, 11, 14, 15 and 16 of the *Hugh M. Smith*. Part B is derived from cruises 2, 5, 7, 8, 9, 11, 14, 15, 16 and 18 of the *Hugh M. Smith* in the equatorial region and cruises 10, 12, 17 and 20 in Hawaiian waters. Part C is derived from cruises 7, 11 and 18 of the *Hugh M. Smith*; cruises 11, 12, 13, 14 and 15 of the *John R. Manning*; cruise 1 of the *Charles H. Gilbert* and cruise 1 of the *Cavalieri*. The vessels *Smith*, *Manning* and *Gilbert* are the property of the U.S. Fish and Wildlife Service. The vessel *Cavalieri* was chartered by the Government for this one fishing cruise. [The number of observations for each interval of latitude is indicated after each bar in the histogram.]

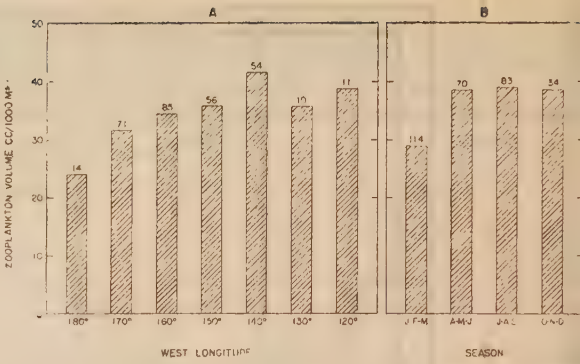

FIG. 4.—Variation in zooplankton abundance wit longitude (A) and season (B), for all observations betwee 9° 59′ N. and 4° 59′ S. latitude. [The number of observations for each longitude and for each season is indicate above each bar in the histogram].

VARIABILITY IN SCALES OF CUTTHROAT TROUT IN MOUNTAIN LAKES

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Abstract

SOME cutthroat trout in mountain lakes fail to establish a year-mark during the first year of life and have scales which are designated as "retarded." Fry which are more advanced in their first fall, have year-marks corresponding to each year of life and are called "normal." The frequency of normal scales was found to be closely correlated (r=.79) with the growth index (quotient of mean length divided by mean age for each sample) in a total of 12 areas.

Introduction

Age studies of some mountain trout species have shown that accurate age determination requires an understanding of the early life history of the species. This was discovered in the course of population studies being conducted on the Yellowstone cutthroat trout, *Salmo clarki lewisi*, by the Rocky Mountain Fishery Investigations. Apparently those fry which hatch in the late summer in some ecological areas may fail to form scales and therefore have no first year annulus. Similar observations were made by Robertson (1947) in his studies on the cutthroat in Wyoming, and by Curtis (1935) in his study of the golden trout in a high California lake.

The interpretation of early scale development in Yellowstone Park was studied in connection with an age composition study of the Yellowstone trout which began in 1953 (Laakso and Cope, 1955). During the examination of the scales, it was observed that some fish had scales of two kinds which differed in the number of perceptible year marks. An earlier study by Brown and Bailey (1952) on scale formation in cutthroat disclosed that cutthroat fry at Yellowstone Park were in various stages of scalation at the end of the first growing season. Owing to the pro-

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[1] The author wishes to acknowledge the advice and materials received from William F. Sigler and Marion Madsen.

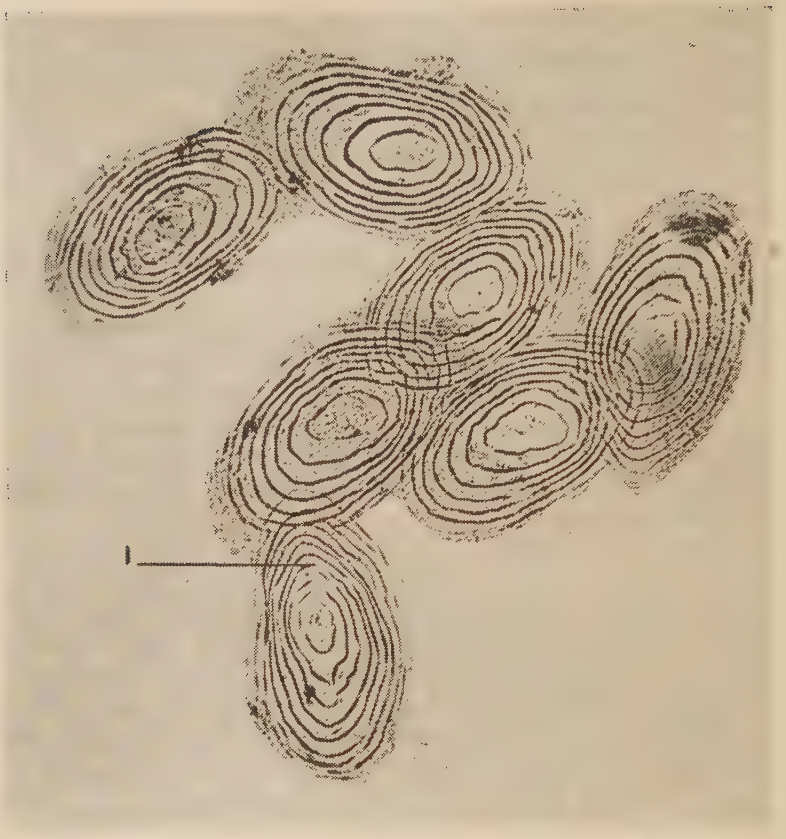

Fig. 1. *Scales from a Yellowstone trout fingerling showing both normal and retarded scales*

longed spawning season, only a part of the 0 age fish were completely scaled at the onset of winter. Some young-of-the-year were partially scaled and a considerable percentage was unscaled. It was therefore postulated that adult cutthroat could be classified into two types corresponding to their first-year development as fry.

1. Normal type

Fish in this group were completely scaled at the end of their first summer and had 4 to 6 circuli with the marginal ones broken and approximated in October or later.

2. Retarded type

Fish in this category have rudimentary scales or none at all at the close of the first growing season, and fail to form a first-year annulus. They are recognizable by the presence of 8 or more circuli (occasionally only 7) before the first annulus. Since scale development originates in the region of the lateral line and on the peduncle, some younger fish were found to be partially scaled at the onset of winter, when scale development either stopped or slowed down. Fry in this category had scales on only a part of the body surface and showed 1 to 3 circuli. Apparently scale growth in these smaller fish stopped abruptly in the fall since no evidence of broken, anastomosed, or approximated circuli could be detected on their scale margins. Circuli added during the following season therefore could not be distinguished from those of the first year except that the total number before the first annulus was usually 8 or more. This was because the scale growth represented more than one year's increment. Some fish of age-group I taken in May had no scales and as adults were usually recognizable by an enlarged focus as well as a larger number of circuli. The appearance of these "open" foci was suggestive of regenerated scales, except that the first circulus had a smooth contour and the expected number of annuli and circuli. Occasionally both normal and retarded scales occurred on the same fish and appeared on a scale mount which usually had four or more scales. This was owing to the pattern of scale development, which proceeds progressively dorsally and ventrally from the plane of the lateral line. If scales from several rows were included in a scale sample, two or more stages of first year scale development were sometimes represented. A photograph of a slide having one normal and six retarded scales from an age-group II fingerling 85 millimeters long taken in Hatchery Creek May 11, 1953, is shown in fig 1. The retarded scales have enlarged foci and 7 to 8 circuli. The normal scale has a poorly defined annulus and a total of 11 circuli.

Since environmental factors appeared to influence the frequency of normal and retarded scales at Yellowstone, a further study of first year scale development in other intermountain waters was made to determine whether the same relation occurred. Data collected by the U. S. Bureau of Fisheries lake stream surveys in 1931-1934, Utah Department of Fish and Game collections, and Rocky Mountain Fishery Investigation materials were incorporated in the study. Scales of fish from 17 locali-

Table 1. *Growth indices and percentages of normal scales for cutthroat trout from various localities*

Locality	Date collected	Number of fish	Growth index	Percentages normal scales
Glacier Park				
Arrow Lake	August, 1934	17	62.2	19.1
Bear Creek	June, 1934	29	59.7	31.0
Fish Creek	August, 1932	11	71.9	36.4
Flat Top Lake	July, 1932	7	70.0	37.5
Howe Lake	June, 1934	29	62.8	41.4
Lower Two Medicine Lake	August, 1932	7	66.5	42.9
Red Eagle Lake	July, 1932	7	96.6	71.5
Utah				
Provo River	August, 1931	20	71.0	50.0
Scofield Reservoir	August, 1933	11	90.6	58.3
Strawberry Reservoir	August, 1933	32	102.8	65.6
Weber River	August, 1931	9	77.7	55.6
Yellowstone Park				
West Thumb	May-June, 1951	59	85.9	43.8

ties (table 1) were studied and classified. While some doubtful scales were discarded, criteria established at Yellowstone for distinguishing normal and retarded scales (Laakso and Cope, 1955) were generally applicable. First year scale growth was slightly greater in some Utah areas than at Yellowstone or Glacier Park; normal scales with as many as 7 circuli before the first annulus were more common in Utah waters. Some collections were excluded from the analysis because of small sample size, their origin as planted fish, or because of the likelihood of hybridization with rainbow trout. Validation of the method for each area was based on the size distribution of normal as compared with retarded fish in each age-group. Further confirmation was obtained from recoveries of known-age planted cutthroat in Navajo and Bridger Reservoirs. Scales from these fish were lent by the Utah Fish and Game Department.

The available chemical and physical data were inadequate for a demonstration of a possible quanitative relation between the amount of first year scale growth and environmental factors. As an alternative to an estimate of the habitat suitability, a calculated growth rate index for each lake or stream was found by

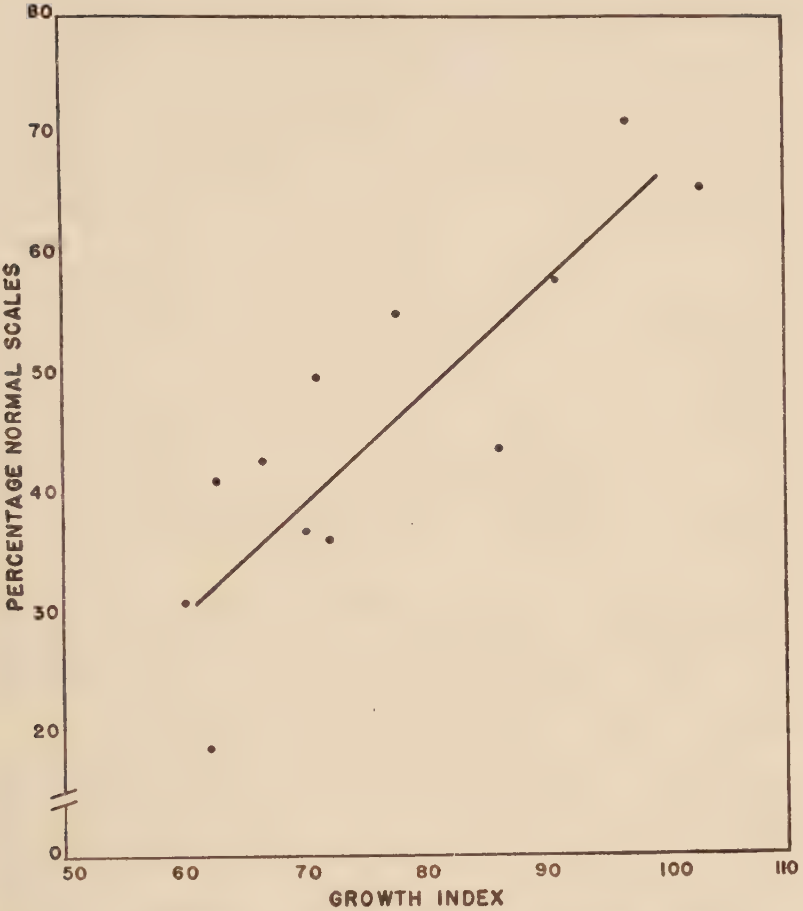

Fig. 2. *The distribution of points obtained by plotting the growth index against the percentage of normal scales for various areas*

dividing the average total length at capture by mean age of fish in the sample. The quotient obtained was assumed to be a measure of the growth-promoting characteristics of a given habitat. The age of normal fish was based on the number of annuli, while the age arbitrarily assigned to retarded specimens was equal to the annulus number plus 0.8 years. Data for this study were limited to fish less than five years old. No correction was made for seasonal differences in time of capture.

In order to study the effect of habitat on scalation, the percentage of normal scales in each area was plotted against the growth index computed for the fish in the area. The resulting scattergram (fig 2) appeared to show a linear distribution for which a straight line was fitted by the method of least squares. The following equation was used: $Y = 28.0 + 1.09X$, in which Y=growth index and X=percentage of normal scales. A 0.79 coefficient of correlation indicated considerable interdependence between growth rate (presumably related to environmental factors) and the frequency of normal scales.

A study of the lake and stream descriptions and data in the survey reports generally showed that the eutrophic areas had fish with better growth and higher percentage of normal scales, while poor growth and predominance of retarded scales characterized fish collected in the more oligotrophic habitats. For example, in Arrow Lake which is represented by the lowest point in fig. 1 a secchi disk was visible at 43 feet on August 13, 1934. A rocky shore with little shoal area and a low bicarbonate concentration accounted for the sparse invertebrate fauna and helped to explain the poor growth and high incidence of retarded scales in the resident fish.

Eagle Lake, which is represented by the highest point in the distribution, gave a secchi disc reading of 12 feet 8 inches on July 5, 1932. This lake had more shoal area, a higher pH, and the factors necessary for an abundant supply of aquatic food organisms, thus providing conditions for better growth.

It is not expected that information on the frequency of normal scales in cutthroat populations will ever supplant the use of conventional growth studies. Data on the frequency of normal scales may, however, provide a convenient corroborative index which in turn will be confirmed by reliable information on growth rate. It is, of course, necessary to distinguish between normal and retarded individuals in any age study where appreciable numbers of fish fail to form annuli after the first growing season. While criteria for distinguishing failure of first-year annulus formation may vary, e.g., at different elevations, the study of adequate numbers of scales provides a basis for differentiating the two types. Fall and spring collections of immatures provide added basis for recognition of normal and retarded scales.

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Ichthyological Notes

the fleshy keel between the anus and caudal fin. Both sexes exhibited deterioration of the eyes, dentition and epidermis.

Examination of a small amount of milt pressed from each of the males demonstrated that spermatozoons in each sample were motile, despite a lack of stimulation by female sex products. Thus, it was assumed that the 12 males were ripe.

The maturity of the 5 female lampreys was tested by gentle stripping. Two specimens from which eggs were readily voided were called ripe; eggs in the remaining females were still bound in ovarian tissue. An attempt was made immediately thereafter to fertilize eggs from the 5 females with milt obtained from the males.

Battery jars containing about ½″ of water were used as receptacles for the eggs and milt. A lamprey was grasped about the head and the thumb was pressed firmly into the oral funnel; the animal was held partly within the container. Eggs or milt were forced from specimens by pressure exerted posteriorly from the branchial region. A male was the first to be stripped, followed quickly by a female. The contents of the jar were stirred thoroughly as the milt from a second male was added. After several minutes the battery jar was filled with fresh water and the mixture let stand.

A separate jar was used to hold the eggs collected from each of the 5 females. Within 1 hour, the eggs were washed and each container was refilled with fresh water. All water used during the experiment came from Lake Huron; its temperature during the incubation period averaged 70° F. (range: 67° to 72° F.).

Evidence of successful fertilization in eggs from the 2 ripe females was first noted in about 4 hours, when initial stages of cell division were observed. In 16 hours, most of the eggs from these two specimens showed multiple cleavage. No sign of cell division could be found in eggs forcibly stripped from unripe females, and after several days they were discarded.

The first ammocoetes hatched 10 days after the eggs were fertilized; most had appeared by 12 days, and the hatching was completed in 16 days. Although no counts were made, a large percentage of the eggs hatched but a great many ammocoetes died soon after. The highly active prolarvae were opaque due to yolk remaining within the body, and growth was rapid. The notochords were prominent and body segments were numerous and well defined.

Thirty of the newly hatched prolarvae were placed in a battery jar which contained about 2 inches of bottom material (sand and mud) taken from a typical larval bed in a nearby stream. Wild, young-of-year ammocoetes were screened from the bottom sediment before it was placed in the jar. The prolarvae squirmed constantly but seemed unable to burrow into the mud. The water was agitated until a covering of sediment settled over them. When the mud was screened 6 days later, only 12 of the 30 specimens were found alive.

Another lot of 92, week-old prolarvae was placed in a large aquarium with a mixture of mud and sand on the bottom. Again the ammocoetes wriggled about on the surface but did not penetrate into the mud. At 2 weeks of age, the yolk inclusions disappeared from their bodies and the specimens became so translucent that they were very difficult to see. Whenever disturbed, they attempted to burrow into the mud but were largely unsuccessful until they were 3 weeks old.

It was impossible to furnish running water to the aquarium, but the standing water was often partially changed and the level was maintained at capacity. After the larvae had been in this tank for 1 month, they were checked for survival; only 9 individuals were found. They had a mean length of 9.9 mm., with a range of 9 to 11 mm. When these survivors were replaced in the aquarium, they promptly burrowed into the mud. The 2 that were still alive 2 months later measured 10 and 11 mm. No further growth was noted when the same pair was measured 3 weeks later at the age of 21 weeks. Observations were concluded at this point because of the small number of specimens and the difficulty of maintaining good water conditions.

The experiment proved that fertile eggs and milt can be stripped from ripe sea lampreys to produce larvae under laboratory conditions. Insofar as I could determine, this was the first attempt made in the artificial propagation of this species.

The present study was conducted at the Fish and Wildlife Service Laboratory, Hammond Bay, Michigan, during 1950. Assistance in the study was contributed by Dr. W. James Leach, Ohio State University.—Robert E. Lennon, *U. S. Fish and Wildlife Service, Kearneysville, West Virginia.*

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The European Oyster in American Waters

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THE common European oyster, *Ostrea edulis* L., which occurs along the Atlantic Coast of Europe from Norway to Spain, in the British Isles, and the western part of the Mediterranean, may propagate at a somewhat lower temperature than our native oyster, *Crassostrea virginica* Gmelin. We thought, therefore, that the European oyster might be introduced into this country (*1*) to occupy eventually a definite ecologic niche in areas where the water is too cold for the successful propagation of our native oyster but is still sufficiently warm to be within the propagating temperature range of *O. edulis*. Among such areas are certain bodies of water along the shoreline of Maine and some well-protected bays and harbors of our Pacific Coast states.

The oysters were shipped to us from the Oosterschelde, Holland, by P. Korringa late in September 1949 and were placed in Milford Harbor on 11 October. The shipment consisted of approximately 9000 oysters representing 3 year-classes, that is, the 1947, 1948, and 1949 sets. Because of the long trip approximately 13 percent died soon after arrival, the mortality being heaviest among the youngest year-class.

The oysters were intended chiefly for studies to determine whether they would survive and propagate under the ecologic conditions to which they would be subjected in this country. Simultaneously with these studies, observations were also made on the seasonal gonadal changes of the oysters kept in different localities, their rate of growth, artificial propagation, and several other aspects of their biology.

Some of the oysters were left in Milford Harbor, but the others were transplanted to four localities of Maine, including Boothbay Harbor. The oysters grew well in all regions. Their mortality in Milford did not exceed, in general, that of the native oyster living in the same environment. Each winter since their arrival from Europe the oysters have lived under a layer of ice, at least for some time. In Milford Harbor, an estuary strongly affected by river discharge, the oysters were subjected, especially in the spring, to prolonged periods of low salinity but, nevertheless, survived, a fact indicating that they possess good tolerance in this respect.

The European oysters were noticeably affected if the turbidity of the water, whether caused by silt or high concentrations of microorganisms, was relatively high. We even witnessed cases of abortion of embryos and immature larvae by gravid females that had been exposed to a dense concentration of dinoflagellates belonging to the genera *Prorocentrum* and *Gymnodinium*. The larvae were expelled in pseudofeces imbedded in mucus along with masses of dinoflagellates. The abortion was usually complete, removing all larvae from the mantle cavity where they are normally carried by the mother oyster. This observation suggests that such a natural phenomenon as the "red tide" may often be responsible for the complete extermination of embryos and larvae of larviparous species of bivalves.

Observations on living individuals and histologic studies of preserved samples showed that the oysters kept in Milford Harbor and in Maine developed normal gonads, spawned, and released larvae. In Milford Harbor larvae-bearing oysters were found from the beginning of July until the end of August. In Boothbay Harbor, where the summer is shorter and the temperature lower, the larvae-producing season is probably correspondingly shorter.

Regardless of the relatively small number of adult oysters planted in Boothbay Harbor, which even at the beginning of the observations was only about 3000 individuals, approximately 50 young oysters originating from the imported parents were found attached to rocks, shells, sticks, and so forth, on the bank approximately ¼ mi from the parents. The young oysters were found confined to the + 1- to − 3-ft tidal level. Judging by their sizes and other characteristics, this group consisted of individuals of three different year-classes, namely, those that set in 1950, 1951, and 1952. In the fall of 1953 the smallest oyster measured was 10.0 mm, but the largest was already 88.0 mm. The finding of so many young, thriving oysters indicates conclusively that European oysters may become successfully established in our waters.

Good growth was also shown by the adult oysters that came from Holland. For example, the largest oyster among the oldest, 1947, year-class, upon arrival here in 1949 measured slightly more than 90.0 mm. In the fall of 1953 some oysters of the same group already exceeded 120.0 mm in size.

Using our methods for ripening mollusks and for inducing their spawning out of season (*2*), we obtained larvae of *O. edulis* throughout the greater portion of the year. Swarms of larvae were released in the laboratory from the beginning of February until the end of the normal spawning season. The larvae were grown through metamorphosis in hatching jars, and in large outdoor tanks with a capacity of several thousand gallons (*3*). Many of these young oysters were later shipped to other places, including the shellfish laboratory of the State of Washington. According to C. E. Lindsay, director of that laboratory, some of this set, which was shipped there in 1951 and planted in North Bay, had reached 77.0 mm in length by August 1954.

Thus our observations have shown that *O. edulis* may survive, grow, and propagate in New England waters and that the young oysters, reared at Milford and sent to Washington, grow well there. They suggest that the introduction of this oyster in certain areas of the United States, and possibly Canada, may eventually lead to the establishment of a new and prosperous shellfish industry.

In introducing a foreign species it should be emphasized that certain precautions should be exercised. First, it should be considered whether the newcomer will engage in biological competition with some of the useful local forms and, perhaps, even displace them from their established niche. A well-known case of such biological competition is the struggle between the highly prized European oyster, *Ostrea edulis,* and the Portuguese oyster, *Crassostrea angulata* Lamarck, which until the middle of the 19th century was confined to the Mediterranean and not found on the Atlantic Coast of France. However, since gaining foothold in the new environment, the Portuguese oyster has rapidly spread throughout a large part of the area formerly occupied only by *O. edulis,* being sometimes responsible for the complete disappearance of the latter in some sections of the coast. The victory of the Portuguese oyster over the native one was ascribed to several factors, of which the chief were that the Portuguese oyster is more prolific, grows faster, and in feeding pumps more water than *O. edulis* (*4*), thus often depriving the European oyster of living space and food.

Another well-known example of an introduced competitor is the small gastropod, *Crepidula fornicata* L., commonly called "slipper-shell" or "quarter-decker" which, in the 1880's, was unintentionally carried along with shipments of American oysters to England, and later extended its range into the coastal waters of western Europe. In both places it quickly multiplied to such an extent that it smothered not only oyster set grown on special tile collectors but occasionally even the beds consisting of adult oysters. The same pest was also introduced to our Pacific Coast where it quickly became a dangerous competitor of the native oyster, *Ostrea lurida* Carpenter.

It is even more important to be certain that, together with the introduced species, we are not bringing along some of the ecologically associated forms which in the new environment may become either serious predators of native commercial species or cause other problems, for example, heavy fouling. An example of the former was the introduction of the American oyster drill, *Urosalpinx cinerea* Say, to our Pacific Coast and to England, and the Japanese drill, *Tritonalia japonica* Dunker, to the oyster beds of our Pacific Northwest. In both places the drills rapidly multiplied and soon began causing heavy losses among the native, as well as the introduced oysters.

A good representative of the second group, one that may cause serious fouling, is the Australian barnacle, *Elminius modestus* Darwin, which recently gained entrance to the waters of Europe and is creating serious difficulties there, being a dominant sedentary organism in the intertidal zone (*5*).

Thus, in principle, the introduction of a new species, whether plant or animal, should always be considered as a potentially dangerous undertaking because of the possibility of bringing along undesirable forms which, in a new environment, could rapidly become pests of major significance, just as the Japanese beetle has become in this country. We think, therefore, that the safest way to build up a population of foreign oysters or other useful bivalves, would be to import a small number of adults, which upon arrival should be kept under such conditions that undesirable forms, incidentally brought along with them, would not gain entrance to the native waters. Later, by using the modern methods of lamellibranch culture (*6*), the spawn of these adults could be used for rearing, under rigidly controlled laboratory conditions, a sufficient number of pest-free individuals for the establishment of initial spawning beds.

References and Notes

1. I wish to express thanks to my colleagues at Milford Laboratory for cooperating with me in many phases of these studies, to the members of the Fish and Wildlife Service at Boothbay Harbor and of the State of Maine Sea and Shore Fisheries who made numerous observations on the oysters planted in Maine, and to C. E. Lindsay of the State of Washington for informing me of the fate of the seed oysters which we shipped there.
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HOW TO INCREASE PRODUCTION OF SEED OYSTERS IN CONNECTICUT

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The study of the time and intensity of oyster setting in Long Island Sound in relation to environmental factors has been one of my chief interests for over 20 years. On several occasions I have had the opportunity of discussing the results of my observations at these conventions, the last being in 1948 when I offered my conclusions based on observations of 12 years covering the period from 1937 to 1948. Since that time, we have added several more years of field observations and have also substantially broadened our knowledge of larvae by studying their behavior under controlled laboratory conditions.

Regardless of the additional material accumulated during the last few years our basic opinion about larvae remains more or less the same as that expressed in 1949. In other words, we think that the oyster larva is a hardy organism and that it can withstand numerous, often quite radical changes in its environment without perishing. We are also quite certain that the intensity of setting of oysters in Long Island Sound is not to any appreciable degree correlated with slight changes in environment which in the past we regarded as extremely important. Among these factors, considered singly and in groups, were temperature, salinity, hydrogen-ion concentrations, solar radiation, precipitation within a water-shed affecting Long Island Sound, and the amount of spawn developed by oysters prior to the beginning of the spawning season. We have also made rather extensive studies of the direction and velocity of the wind, but so far have found no correlation indicating that they reflect upon the intensity of setting.

On the other hand, our laboratory studies of larval behavior, especially their food requirements, some of which have already been reported at this convention by my associate, Harry C. Davis, and by me have shown that oyster larvae, unlike those of many other bivalves, are unable to survive on most planktonic forms fed to them. This leads us to believe that perhaps in nature oyster larvae may have difficulty in finding nannoplankton that they can take in and assimilate. The relative absence of such forms in some years or in certain areas, or the difference in their numbers, may be responsible for fluctuations in the intensity of oyster setting from year to year.

As already pointed out in some of my articles, the years of good oyster sets in Connecticut waters are quite uncommon. I base this conclusion on the records of the State shellfish authorities,

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information which was kindly supplied to me by oyster companies which have been operating since before the turn of the century and, finally, from my own observations which cover almost a quarter of a century. For example, these records show that between 1904 and 1925, a period of 21 years, not a single general, heavy set occurred in the Sound. During this period the industry survived by buying abundant seed oysters that grew on so-called natural beds which were located mostly in shallow inshore waters. Since 1925, we have had good sets only on five occasions, i.e., 1930, 1939, 1940, 1944 and 1945. In other words, in the last 54 years we have had only six or perhaps seven good, general sets. The remaining years were either complete blanks or so-called marginal years, i.e., years during which a general, light set occurred in the Sound, or when good sets occurred in some sections but in other areas setting was a failure, as happened in 1953, when only the Bridgeport area caught a good set.

Let us imagine a farmer who would gather a commercially profitable crop only every eighth or ninth year. How long could he continue to exist? Should he not look for other tracts of land where more regular and more abundant crops could be grown? I think he should and I also think that the Connecticut oyster industry, imitating a wise farmer, should also consider the possibility of transferring a substantial portion of its seed oyster production operations from the open Sound to more promising areas. Please notice that I do not advocate a complete change, i.e., abandonment of the oyster beds in Long Island Sound proper. I merely suggest the extension of our oyster cultivating efforts into shallow, more protected waters where conditions for production of seed are more promising.

Let us begin to discuss the necessity of this move by admitting that most of the conditions affecting the oyster industry of the Sound proper are virtually uncontrollable. These conditions may be either of physical or biological nature. The most outstanding examples of the former are our highly destructive storms. The industry still remembers that of November, 1950, which killed millions of oysters, ruined many beds and placed several oyster companies on the verge of bankruptcy. Nothing could have been done to prevent this catastrophe because the storm came without warning.

Of the biological factors we would probably think, first of all, of such well known enemies as starfish and drills. It is true that they may be eliminated from small areas by the persistent use of lime, mops or suction dredges, but they will continue to invade the beds from the surrounding grounds which remain uncleaned. Furthermore, as is well known, starfish have pelagic larvae, which are carried around by the currents and which may set in immense numbers on an oyster bed regardless of how free of adult starfish the bed is. We know many cases of this nature. We may also mention several formerly extremely productive oyster setting areas which were eventually given up because it became economically unprofitable to defend these beds against the enemies.

Thus, it is clear that the open Sound is not only an unreliable place for getting sets regularly but also a place where if the set does occur, it remains difficult and expensive to protect against enemies. The question that naturally arises because of these considerations is what the industry could or should do to place itself in a more advantageous situation. The answer may be that a partial solution of this problem should consist in the utilization of numerous bays, harbors, and deltas of rivers where extensive natural beds of oysters existed in the past, but which at present are barren and useless.

What are the advantages of gravitating towards inshore areas? There are several important ones. To begin with, our observations, as well as those of our predecessors in biological phenomena, show rather clearly that oyster set rarely fails in inshore waters. We estimate, for example, that in Milford Harbor and Indian River, if they were properly planted and managed, a set of commercial importance could be gotten nine out of every ten years. Furthermore, beds located in bays and harbors would be better protected against storms. Finally, because the salinity of the water in many inshore areas where oyster beds could be established is comparatively low, the oysters, especially young set, would be protected by nature itself against starfish and drills, which require a comparatively high salinity to exist and propagate. This consideration alone is of tremendous practical significance because it eliminates from the debit side of the companies' ledgers astonishingly high sums of money spent on pest control.

A criticism of our suggestion may be offered by pointing out that most of the inshore waters are more heavily polluted, industrially and domestically, than Long Island Sound proper. This should be admitted, but since the Connecticut industry is chiefly concerned with seed oysters which will not be sold for several years, the matter of sanitation does not enter into the picture. Furthermore, our observations indicate that, as far as tolerance to domestic and industrial pollution is concerned, oyster larvae and young set may be hardy organisms. I base this conclusion on observations familiar to all of us from Connecticut that heavy sets have often occurred in the Quinnipiac River in New Haven, Poquonock River, Bridgeport, and Housatonic River, which drain the most heavily industrialized areas of our State. We may also recall that during 1944, when all our industries were at their maximum production for the war effort, and when due to the inflow of hundreds of thousands of industrial workers the problem of domestic pollution became rather acute, we had one of the best oyster sets since 1900. Yet, we have to admit that during this year there was more pollution entering our waters than normally. This, of course, does not indicate that pollution is desirable or harmless to oyster larvae. It simply shows that larvae possess quite a tolerance and, therefore, rivers which are slightly polluted should be considered among the areas capable of procuring heavy sets. Furthermore, if the trend toward abatement of pollution developing so well during the past 25 years should persist, and we have reason to believe it will, pollution may not be a problem at all.

The chief obstacles to the utilization of natural oyster producing bottoms are, in my opinion, the archaic regulations many of which were passed more than a century ago, and which designated most of the inshore waters as public grounds. In other words, those areas cannot be rented to private individuals or companies for cultivation of shellfish. These regulations, which in the past perhaps were desirable, have eventually led to the present condition where we find the majority of our potentially most productive oyster areas virtually barren due to lack of care. Thus, from economical and biological points of view these areas are now entirely wasted. Since there is practically no one making a living from these areas, logically, no one would suffer if some of these beds were leased for cultivation to private individuals or companies. By proper cultivation of these areas the industry would become assured of an abundant annual supply of oysters, and the township in the State would gain additional revenue.

In connection with this discussion we should add that utilization of numerous shallow salt water ponds should also constitute part of the program which I suggest. Some of the ponds in Martha's Vineyard have proven quite productive and the studies which we initiated with the help of some Connecticut oyster companies along the same line suggest that such ponds may eventually be utilized not only for the production of seed oysters but also clams.

Several technical problems will have to be met in connection with moving some of the industry's activities into shallow inshore waters because the methods to be employed there would necessarily differ from those used in the open Sound. I am sure such problems would be rapidly solved by our oystermen who have been capable of designing and placing in operation such complicated mechanical devices as the suction dredges now operating in the Sound.

FOOD REQUIREMENTS OF SOME BIVALVE LARVAE

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U. S. Fish and Wildlife Service, Milford, Connecticut

Almost at the very beginning of our work with bivalve larvae we began to suspect that the various species differed in their feeding behavior and had widely different food requirements. With more experience in culturing larvae and more knowledge of their behavior we concluded that, in general, the larvae of all the species that we have grown thus far, and they number 16, can be roughly divided into two groups. The larvae of the first group, probably best represented by oysters of the genus Crassostrea, which includes our Atlantic oyster, C. virginica, and the Japanese oyster, C. gigas, are able to utilize only a few of the many food forms which are fed to them (Davis, 1953). The second group, represented by larvae of the clam, Venus mercenaria, or the common mussel, Mytilus edulis, seems, on the contrary, to thrive on most micro-organisms provided they are small enough to be ingested (Loosanoff and Davis, 1950).

The difference in the food requirements of these two groups was clearly demonstrated several years ago both in laboratory experiments and in outdoor tanks (Loosanoff, 1950). In these experiments the larvae of the clam, Venus mercenaria, and the oyster, Crassostrea virginica, were kept together in the same jars or tanks, and were, therefore, under identical conditions. They received the same food consisting of mixed nannoplankton in which the cells of small green algae predominated. The larvae of V. mercenaria grew rapidly and metamorphosed in about 13 days, while those of C. virginica showed virtually no growth after attaining the straight hinge stage and, eventually, died without any appreciable increase in size.

The experiment was varied by changing the relative numbers of larvae of the two different species and by offering different quantities of food. Nevertheless, in all these experiments the larvae of the clam grew rapidly and metamorphosed, but the oyster larvae showed no growth. Apparently the latter were unable to utilize the food forms that were abundant in the surrounding water and which were, obviously, assimilated by the clam larvae.

Another circumstance which attracted our attention during the early stages of our work with larvae was that their survival and rate of growth depended, to a large extent, upon the quantity of food cells present in the water. On many occasions the larval cultures were killed by what appeared to be overfeeding. On others, the rate of growth was abnormally slow, probably because of an insufficient quantity of food. Obviously, to succeed in growing larvae with consistent results their quantitative and qualitative food requirements had to be ascertained.

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olume 45, pp. 66-83, 1955.

The food requirements may vary with the species of larvae, their age, or with the species of the food organisms themselves. Because of our limited personnel, we could not undertake studies of the food requirements of all the species of larvae with which we worked. Instead we confined our work to a few selected forms, which we believe to be representative of much larger groups of bivalves. In this report we shall describe some of our experiments on clam larvae that we think are of general interest.

We may begin by repeating, what has already been reported by us in various articles, that contrary to the generally accepted view advanced by Blegvad (1915) we found no evidence that organic detritus is utilized by larvae of clams (Loosanoff, Miller and Smith, 1951) or oysters (Davis, 1953). On the other hand, while clam larvae seem to be able to grow on sulfur bacteria, oyster larvae can utilize neither sulfur bacteria nor any other of the 13 species of marine bacteria isolated for us from the sea water of Milford Harbor by Dr. Burkholder formerly of Yale University. These results are rather interesting because they contradict another old and generally accepted, although unverified, point of view, that marine bacteria constitute an important part of the oyster diet.

As may be remembered, Davis (1953) showed that young oyster larvae cannot utilize green algae, such as Chlorella, while larger larvae of the same species, after reaching the size of about 125 u, are able to do so. We had already made many observations indicating that larvae of several species, such as *Venus mercenaria*, *Mya arenaria*, *Mytilus edulis*, and even the European and Olympia oysters, can be grown on a diet consisting chiefly of *Chlorella* (Loosanoff and Marak, 1951). Davis' experiments, however, definitely proved that bivalve larvae are able to utilize certain green algae. This conclusion was supported by another series of experiments in which clam larvae were grown on a unialgal culture of *Chlorella*, reaching metamorphosis in about 12 days. Since this alga was isolated from the sea water of Milford Harbor, it probably constitutes part of the normal diet of the larvae of this region. Further experiments showed that clam larvae also grew well, reaching metamorphosis, on pure cultures of any one of the following three flagellates: *Chlamydomonas sp.*, *Chromulina pleiades*, or *Isochrysis galbana* (Davis and Loosanoff, 1953).

These studies demonstrated two important points, namely, that clam larvae can live and grow on a very restricted diet, actually consisting of a single species of algae, such as *Chlorella*, or flagellate, and that unlike oyster larvae they can utilize green algae during all stages of development. Our conclusions, obviously, differ from those of some European workers (Cole, 1936) who maintain that bivalve larvae do not possess certain enzymes needed for the digestion of cellulose of which the cell walls of algae, such as *Chlorella*, are made and, therefore, cannot survive on such a diet.

The next problem was to determine the effect of different concentrations of certain food organisms upon the rate of growth and survival of larvae. From some of our early experiments we already knew that if fed approximately 200,000 to 300,000 cells of small *Chlorella*, measuring only about 3 u in diameter, per cc. of water, the larvae would live and metamorphose. However, we did not know whether the optimum concentration of food cells would be above or below this range. To answer this question a series of cultures of larvae of *V. mercenaria*, each containing approximately 6.5 individuals per cc., were given different quantities of food. The principle foods tried were a mixed culture of plankton consisting largely of small *Chlorella*, measuring only about 3 u in size, and a unialgal culture of large *Chlorella*, the cells of which averaged about 8 u in diameter.

As was shown by the increase in size and survival of the larvae, the optimum concentration of food depended upon the size of the food cells (Loosanoff, Davis, and Chanley, 1953). When large *Chlorella* was used the optimum concentration was approximately 50,000 cells per cc. (Fig. 1). However, approximately 400,000 cells per cc. of smaller cells were needed to maintain the growth of the larvae at an equal rate.

The difference between the length-frequency distribution of the larvae in cultures that were given the optimum concentration of food and those that were somewhat overfed is illustrated in Figure 2, which shows that the larvae given approximately 400,000 cells of small *Chlorella* per cc. were, at the end of the tenth day, considerably larger than those that were fed approximately 750,000 cells. As can be concluded from the similarity of the two curves, the data also suggest that the food value of 400,000 small *Chlorella* closely approaches that of 50,000 cells of the larger form. Were we to assume that the cells of *Chlorella* of both species were perfect spheres, the largest measuring 8 u and the smaller about 4 u in diameter, we would find that regardless whether we fed 50,000 cells of the large form or 400,000 of the small, the total volume of cells in one cc. of water containing larvae would be approximately $13.40 \text{ x } 10^{-3}mm^3$. Carrying this comparison further we may calculate that 750,000 cells of the small form have a total volume of $25.13 \text{ x } 10^{-3}mm^3$., which closely approaches the volume of $26.81 \text{ x } 10^{-3}mm^3$. of 100,000 large cells. As can be seen from Figure 1, the larvae fed these quantities of the two foods grew at approximately the same rate, and both cultures showed signs of overfeeding. It would be interesting to determine whether the addition of a similar volume of other food forms per cc. of water would enable larvae to grow at the same rate.

The larvae were usually killed when the concentration of food cells became too heavy. This concentration depended again upon the size and kind of cells. For example, a concentration of about 300,000 cells of large *Chlorella* per cc. of water killed approximately 90 per cent of the larvae within a few days and those that survived grew very slowly or not at all, as did the larvae in the unfed control. The volume of 300,000

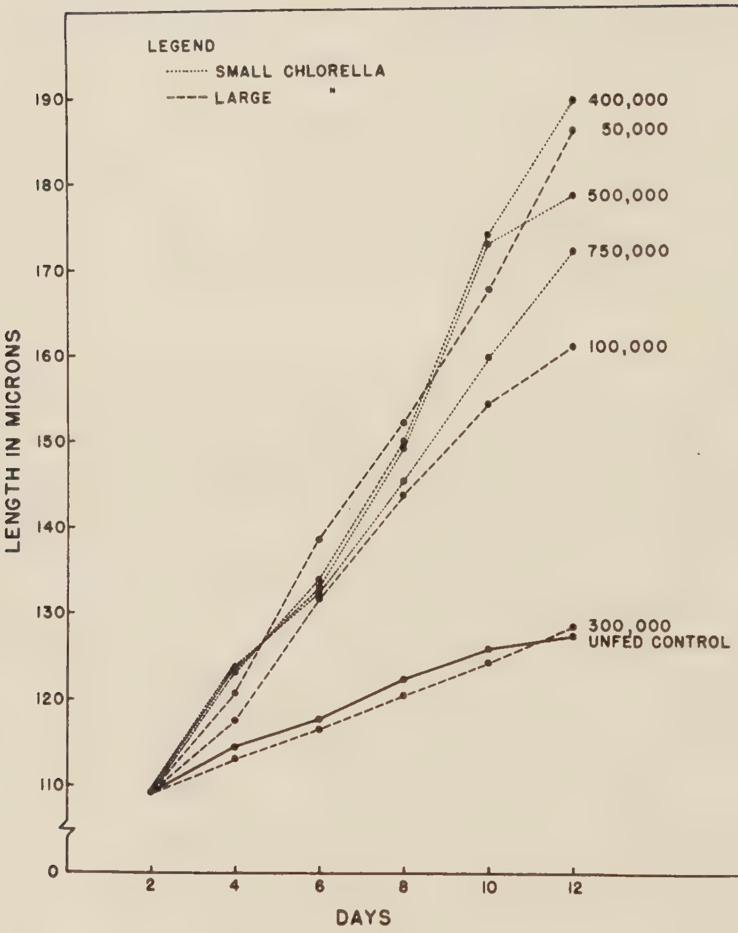

Fig. 1. Mean length of larvae of hard clam, Venus mercenaria, of different ages in cultures kept at the same population density of 6.5 larvae per cc. but given different numbers of cells of small or large Chlorella per cc. of water.

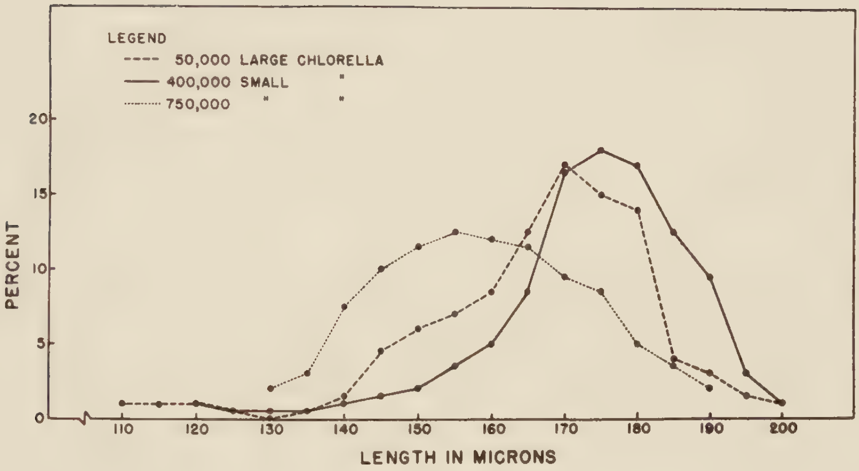

Fig. 2. Length-frequency distribution (expressed in per cent) of ten day old larvae in cultures kept at the same population density of 6.5 larvae per cc. but given different numbers of cells of small and large Chlorella.

cells of large Chlorella is approximately 80.43 x $10^{-3} mm^3$. When the concentrations of large Chlorella were increased to approximately 500,000 or 700,000 cells per cc. total mortality occurred sometimes within 24 hours. However, when fed the much smaller form of Chlorella the larvae survived and grew comparatively well in concentrations as high as 750,000 cells per cc. (Fig. 1).

The larvae surviving in heavily fed cultures usually displayed some anatomical abnormalities which often made the larvae unable to ingest the food. Perhaps these abnormalities were to some extent responsible for the survival of such larvae under conditions which were lethal to normal ones.

In discussing the effects of certain concentrations of food organisms upon the growth and survival of larvae it should be remembered that the number of cells given constitutes only one approach for estimating the value of the food form. It has been pointed out by other workers (Burlew, 1953) and it has also been noticed by us on numerous occasions, that the food value of such forms as Chlorella may show considerable variations according to the age of the culture, its density of population, and, of course, the media in which it is grown. While trying to standardize as many factors as possible in our feeding experiments we still have not tried to feed the larvae with Chlorella cultures of one age only.

Comparable to the effects noted in adult oysters by Loosanoff and Engle (1947) we found that clam larvae may be killed either by the cells alone or by the filtrate only of the food culture or, of course, by a combination of the two (Loosanoff, Davis, and Chanley, 1953a). Dense concentrations of the food affect the larvae both mechanically, by the cells interfering with the swimming and feeding mechanism, and chemically, by the accumulated metabolic products of the cells which are toxic to the larvae. For example, in an experiment in which the larvae were kept in millipore filtered sea water, the larvae grew well in a culture receiving 100,000 large Chlorella cells per cc., plus the media in which the Chlorella was grown, even though this concentration was somewhat above the optimum (Fig. 3, A). However, both the larvae receiving cells alone, filtered off by use of a millipore filter and resuspended in sea water, at the rate of 1,000,000 cells per cc. (Fig. 3, D) and the larvae receiving the filtrate only from the above cells (Fig. 3, E) soon died. The results indicate that the filtrate containing metabolites of the cells may be more detrimental than the heavy concentration of the cells themselves. This toxicity of the so called external metabolites and their ecological effect have long been recognized by aquatic biologists (Lucas, 1947).

In this experiment the larval culture receiving filtrate from relatively small quantities of Chlorella grew somewhat better than the unfed control, especially during the first few days of life of the

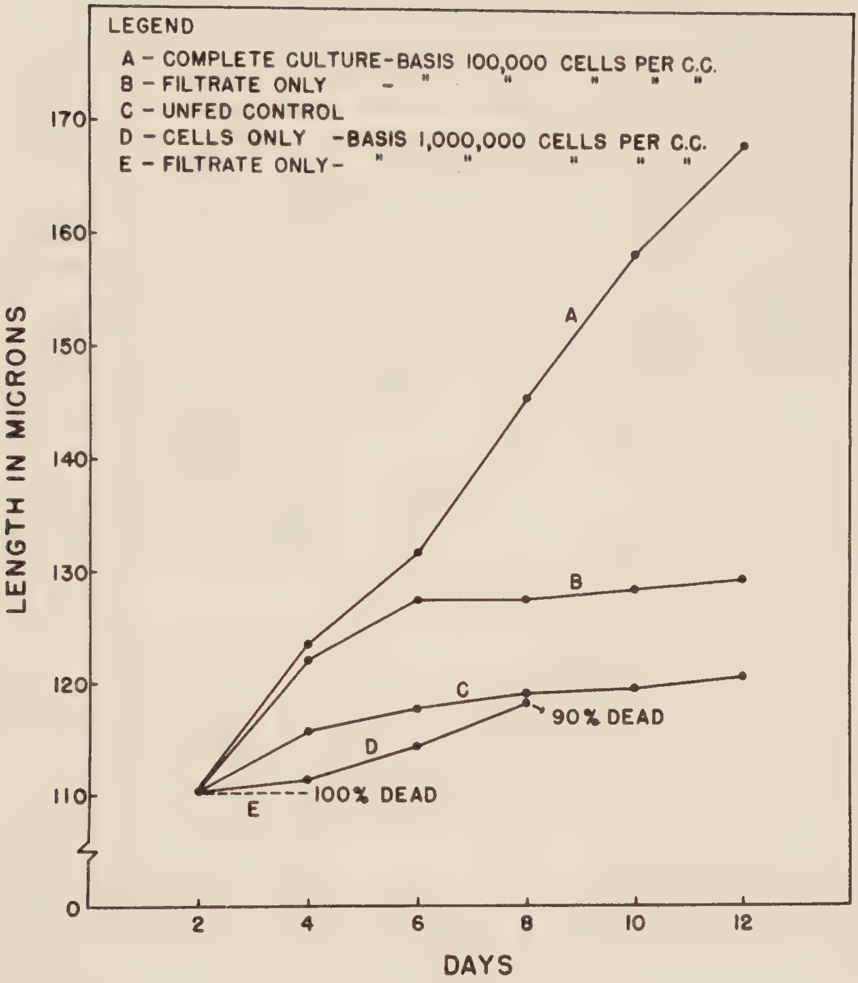

Fig. 3. Effects of whole culture of Chlorella, of cells alone, and of the filtrate only at two concentrations upon growth of larvae of Venus mercenaria.

larval culture (Fig. 3, B, C). Additional experiments will be needed to determine whether this growth was due to the suspended matter present in the water or to the ability of the larvae to utilize some of the dissolved substances in the filtrate.

In observing the behavior of clam larvae we noticed that they showed both mechanical, or quantitative, and chemical, or qualitative, selectivity in feeding. By regulating the amount of food ingested the larvae kept in heavier-than-optimum, but still nonkilling concentrations of food cells, often contained less food in their stomachs than the larvae in lighter food concentrations. This suggests that larvae are not merely mechanical feeders but possess a mechanism by means of which they can control the food intake. Nevertheless, if kept in a heavy concentration of food cells for a long time, the larvae lose this regulating ability and soon become choked with food cells. However, if these larvae were removed to clear sea water, they would, if not too seriously injured, expel the excess ingested food and continue to develop and grow normally if properly fed.

The ability of larvae to select food was observed when they were given a mixture of several food organisms but showed definite preference for one of them. As an example, given a mixture of *Porphyridium* and *Chlamydomonas* the larvae ingested the much larger cells of *Chlamydomonas* while rejecting the small cells of *Porphyridium*.

Another problem was to find the optimum concentrations of larvae that should be maintained in the cultures. In the early stages of our work it appeared that if cultures are properly attended and fed, the majority of the larvae even in rather dense cultures will survive and, although displaying a slow rate of growth will, nevertheless, reach metamorphosis. We now know that to some extent optimum, as well as maximum, concentrations of larvae depend upon the species, but such hardy varieties as *V. mercenaria* can be grown having as many as 50 larvae per cc. of water. Although this is a much heavier concentration than those advocated by other investigators, who usually emphasize the danger of overcrowding, we have frequently reared larvae to metamorphosis in such densities and, on many occasions we have successfully grown even denser cultures. We believe that, as far as carrying the larvae of some species to metamorphosis is concerned, the danger of overcrowding may not be as acute as believed. This opinion is shared by our colleague, Melbourne R. Carriker, of the University of North Carolina, who has also succeeded in growing cultures of *V. mercenaria* at the above mentioned concentrations (personal communication).

To verify our impression, and at the same time learn more about the effect of crowding upon larvae a quantitative experiment was designed to determine the survival and rate of growth of larvae in different concentrations (Loosanoff, Davis, and Chanley, 1953b). Larvae of *V. mercenaria* were grown in concentrations of about 6.5, 13, 26 and 52 early straight hinge larvae per cc., with each culture receiving the same quantity of food, namely, 100,000 cells of large *Chlorella* per cc. The larvae in all cultures showed a low rate of mortality and grew to metamorphosis. However, the mean rate of growth of the different cultures had an inverse relation to the population density (Fig. 4). For example, on the tenth day the mean length of the larvae in the series of cultures containing 6,6.5,13, 26, and 52 individuals per cc. was 162, 156, 151 and 144 u respectively. On the 12th day the difference between the two lightest cultures was even more pronounced.

It is assumed that the slower growth in the more crowded cultures was caused by more frequent collisions between the larvae, which interfered with the feeding, by the deleterious effects of the greater concentration of the excretory products of the larvae accumulating in the water and, at least during the later stages, by competition for food.

The effects of crowding were further demonstrated by the experiments in which the cultures containing either 6.5 or 32.5 larvae per cc.

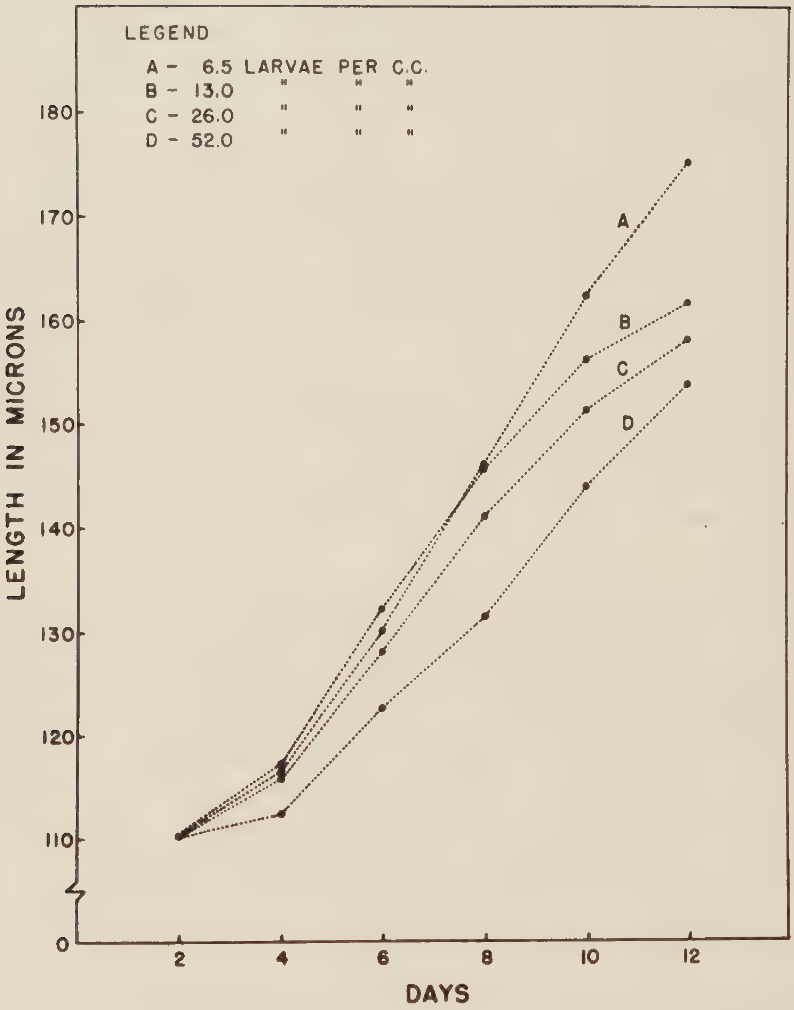

Fig. 4. Mean length of larvae of Venus mercenaria of different ages in cultures kept at different population densities but receiving the same quantity of food per cc. of water (100,000 cells of large Chlorella).

were given what are considered optimum quantities of two kinds of food cells. Some cultures received 50,000 cells of the large Chlorella, while the others received 400,000 cells of the smaller form (Fig. 5). The cultures containing 6.5 larvae per cc. grew quite rapidly on both kinds of food. The more crowded cultures, containing 32.5 larvae per cc., grew well between the second and fourth days suggesting that there was sufficient food for this number of larvae at this size, but grew much more slowly during later stages. At the end of 12 days they averaged only about 147 u, as compared with 189 and 185 u for the two lightly populated cultures.

The discrepancy in the sizes of the larvae of the cultures widely differing in population density is further emphasized by comparing the length-frequency distribution of the larvae. We may take as an example the cultures shown in Figure 5 that received 50,000 cells of large Chlorella but differed in population densities. By plotting the length-frequency distribution of the larvae of these cultures at the end of the tenth day one can easily see that while the modal class of the lightly populated culture was approximately 170 u, that of the denser culture was only about 145 u (Fig. 6). Furthermore, while the maximum size of the larvae in the first culture was at that time already 200 u, the largest larvae in the more crowded culture measured only 175 u. It was also noticed that the range of lengths of the larvae was much greater in the lightly populated than in the denser cultures. Earlier Davis (1953) came to the same conclusion in his studies of oyster larvae, C. virginica. These experiments showed that, as we thought previously, clam larvae will grow and reach metamorphosis even if heavily overcrowded (Loosanoff, Miller and Smith, 1951). However, present observations indicate that, contrary to our earlier opinion, the larvae in such overcrowded cultures will reach the setting stage later than those in less populated cultures.

As a result of our experiments on crowding of larvae, the question arose whether the growth of larvae in overpopulated cultures could be maintained at the same rate as in lightly populated ones by increasing the quantity of food proportionally to the increase in population. Accordingly, experiments were conducted in which the increase in the larval population was accompanied by a proportional increase in the number of food cells. The cultures containing approximately 6.5 clam larvae per cc. were given 100,000 large Chlorella cells per cc. per day; the cultures containing 13 larvae received 200,000 cells; 26 larvae received 400,000 cells and, finally, the cultures with 52 larvae were given 800,000 cells per cc. per day (Fig. 7).

At the end of the 14th day the larvae in the least crowded culture averaged almost 190 u in length and many of them were already metamorphosing. In the next least crowded culture, containing 13 larvae per cc. of water and receiving 200,000 cells of large Chlorella per cc., the larvae averaged only slightly over 150 u, even though the same number of food cells per larva was available as in the first culture. A majority of the larvae given 400,000 cells of Chlorella per cc. died within four days. Those fed 800,000 cells per cc. died within 48 hours,

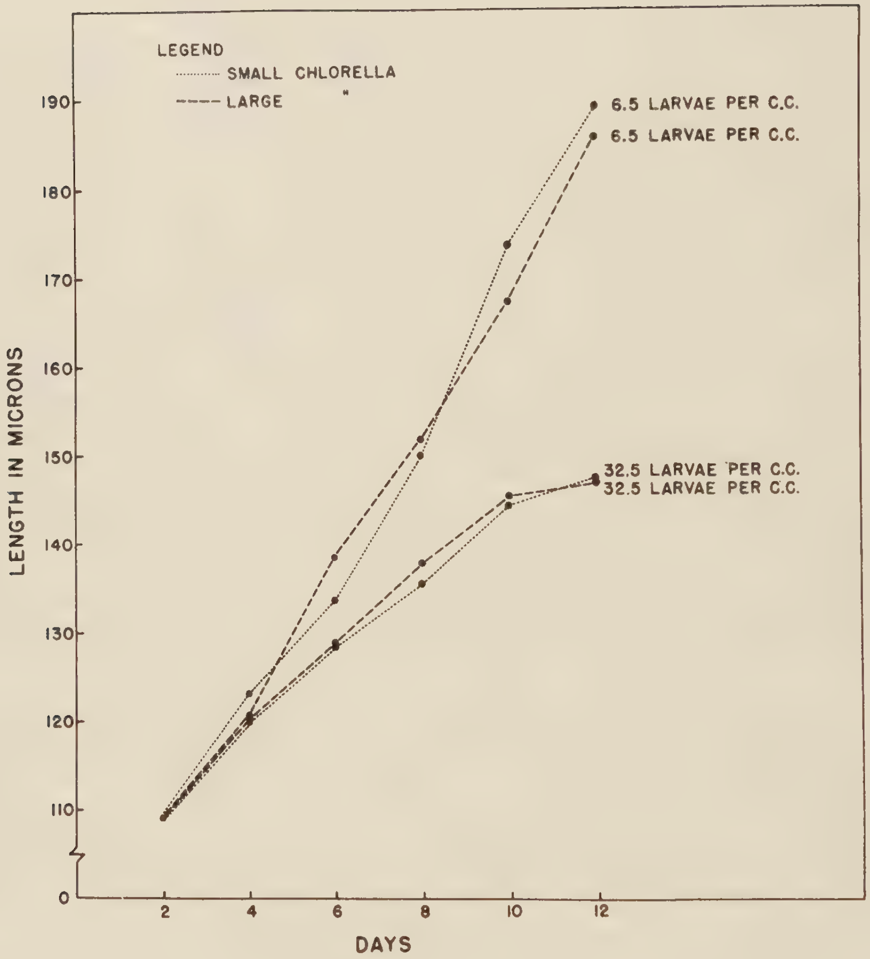

Fig. 5. Mean length of larvae of Venus mercenaria of different ages in cultures kept at two different population densities but given the same quantities of food. The foods were 400,000 small or 50,000 large Chlorella cells per cc.

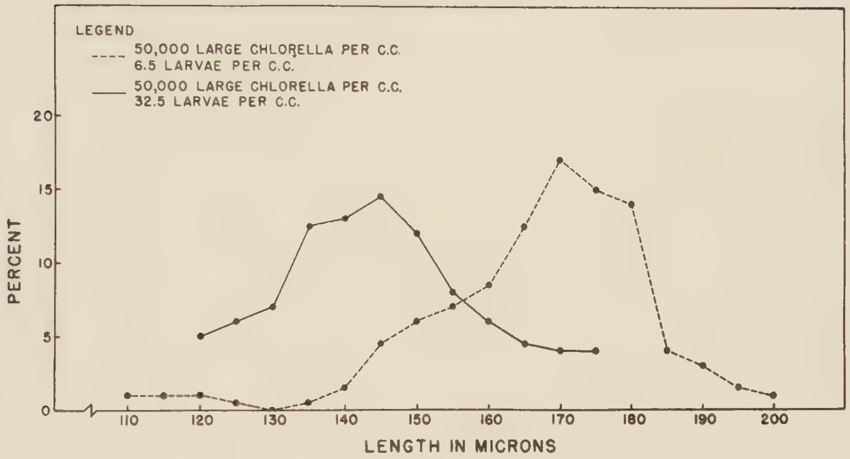

Fig. 6. Length-frequency distribution (expressed in per cent) of ten day old larvae of Venus mercenaria in cultures maintained at different population densities but fed the same quantities of food.

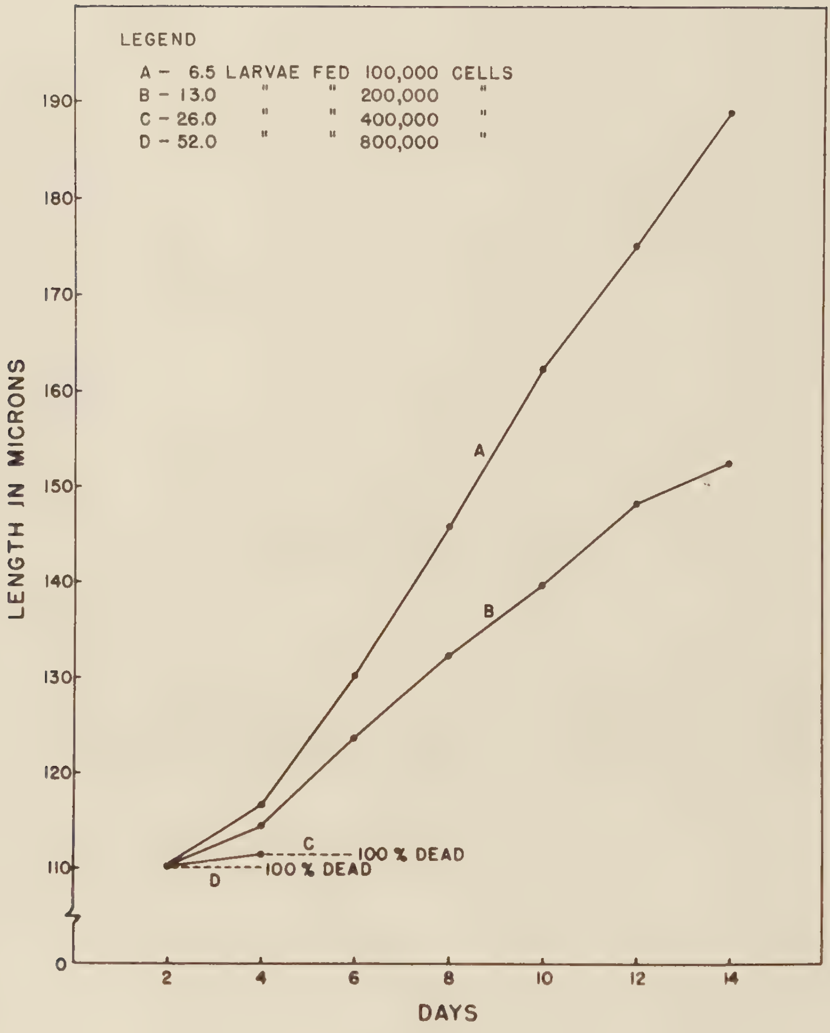

Fig. 7. Effects of increase in food concentrations (large Chlorella) made in proportion to increase in density of larval population upon growth and survival of larvae.

the majority succumbing within the first 24-hour period of heavy feeding. This and similar experiments have demonstrated that an increase in the larval population beyond certain limits cannot be compensated, as far as rate of growth and survival are concerned, by a proportional increase in the quantity of food made available.

On some occasions, recently developed early straight hinge clam larvae were kept in cotton filtered sea water without receiving additional food for as long as 14 days. The growth of these larvae was, as a rule, considerably slowed down or entirely arrested, but the larvae themselves remained normal in appearance and continued to swim. If after such a long period of virtual starvation the larvae were given food, they began to grow and eventually reached metamorphosis. Obviously, clam larvae can endure a near starvation diet better than overfeeding.

As may be concluded from this short report, the studies of clam larvae have already considerably added to our understanding of the behavior of these organisms, placing us in a position where we can now decide what, from a practical point of view, should be the most advantageous ratios in our cultures between the numbers of larvae and numbers of food cells of certain kinds. Future experiments should be directed towards making such ratios even more accurate by introducing a progressing correlation factor that would compensate for the increase in the size of the larvae during the life of a culture.

We hope the information on the effects of temperature on the rate of growth of larvae (Loosanoff, Miller and Smith, 1951), together with the present data concerning the optimum ratio of food to larvae, will soon give us definite formulae indicating the most advantageous combinations of these factors for growing the largest number of clam set in the shortest time in small volumes of water. Even now, utilizing our present limited experience, we are able to grow to metamorphosis approximately 1,000,000 small clams per month per five-gallon jar the bottom area of which is only about one square foot (Fig. 8). Our present methods allow us to grow clams during the entire year. Therefore, we can roughly estimate that a single jar can be used to grow approximately 12,000,000 clams per year provided we can keep mortality at a low level.

Although we still do not know of any efficient method for controlling fungi, such as Sirolpidium, which at times causes heavy mortality among our larvae, we are optimistic enough to think that we may easily prevent and control many bacterial and, perhaps, virus diseases which we suspect to be prevalent among the larvae. Our optimism is founded on the results of some of our preliminary experiments in which larvae were kept in water to which certain quantities of sulpha drugs or such antibiotics as procaine penicillin G or chloromycetin were

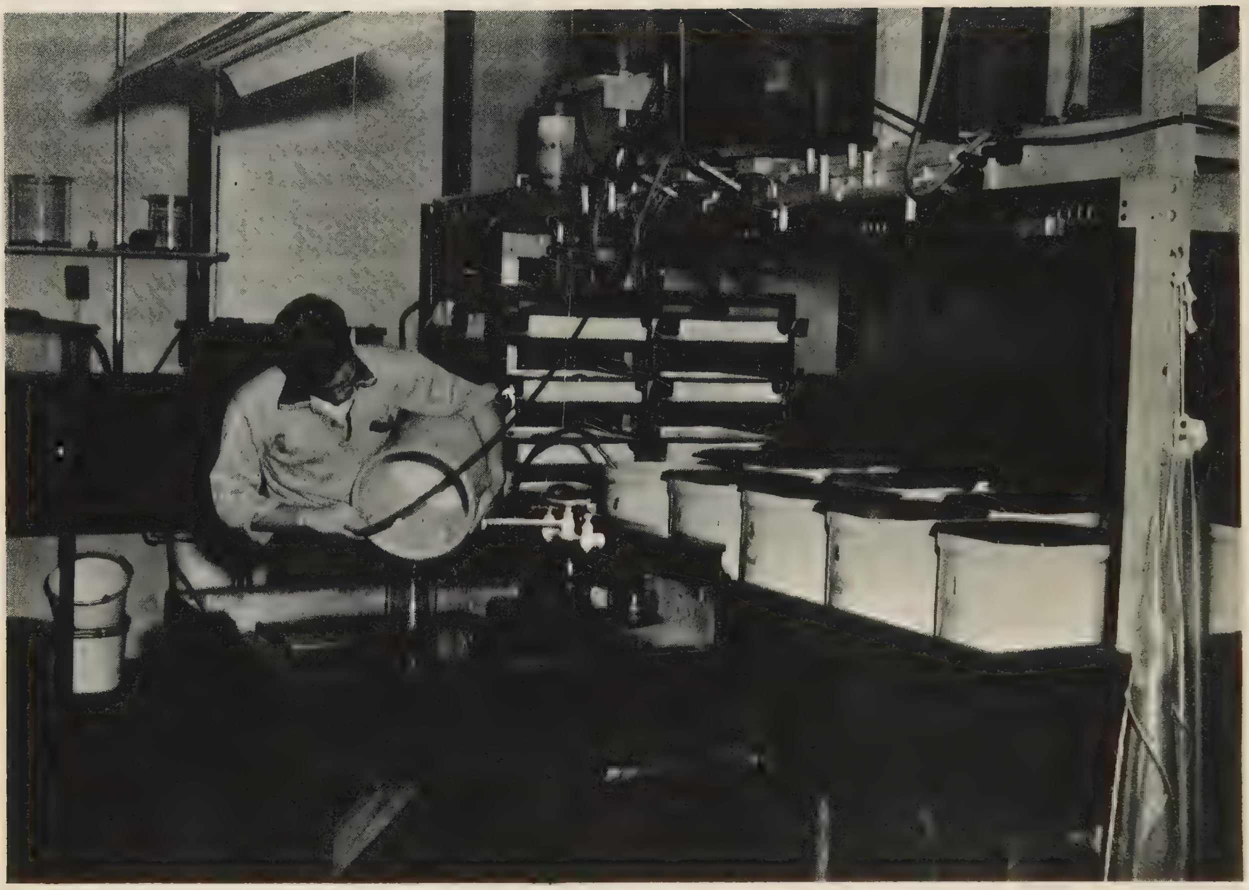

Fig. 8. Battery of jars for rearing bivalve larvae.

added. Mortality of the larvae in cultures so treated was usually lower than in the controls. Further studies in this field will be conducted at our laboratory.

Clam sets obtained by the use of our methods should be free of the admixture of juveniles of other bivalves, which in the early stages look almost the same as small V. mercenaria, and which later on will have to be removed, a slow and expensive process. The clams will also be free of external enemies, such as crabs, or borers, the larvae of which may set in nature simultaneously with clams. Finally, the set will originate from known stock or, if necessary, even from known pairs of parents, as has often been done at our laboratory. From then on, if we learn how to control diseases of larvae and juvenile clams, the breeding of clams of desired qualities, such as rapid growth, high glycogen content, and resistance to certain diseases, will become commercially feasible.

We wish to express our appreciation to our colleague, Charles A. Nomejko, for participating in some aspects of these experiments and for making the illustrations for this article, and to Miss Rita Riccio for her generous help in editing and preparing the manuscript.

10-, 20-, and 30-foot depths and their number in the different years varied from seven to 18. Since 1944, however, the number of stations has always been ten and their locations have remained the same.

At semi-weekly intervals the collectors were removed from the stations and brought in moist condition to the laboratory for examination. Using a low-power dissecting microscope the oyster set was counted on ten shells selected at random from each bag, and then the same ten shells, plus an additional ten shells, were examined for the presence of starfish set. The results were later expressed as the number of set of each species per 100 shell-surfaces. Counting of set was done only on the clean inside surfaces of the shells.

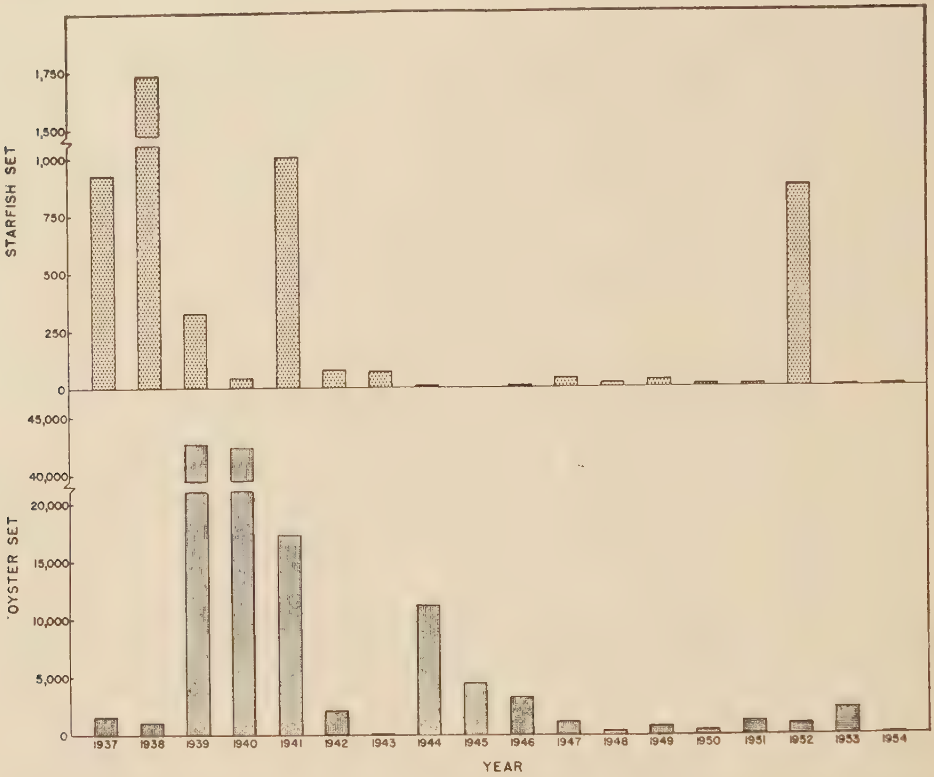

FIGURE 1. Average numbers of oyster and starfish sets per station recorded in different years on 100 shell-surfaces. Long Island Sound, 1937–1954.

Each time a bag was removed from the water it was immediately replaced by a new one with unused shells. To obtain more reliable data we used, as a rule, two bags at each station, and averaged the results. The period during which the observations were made usually extended from the beginning of July into October, covering, therefore, the entire setting season of both species.

The intensities of the oyster and starfish sets in the different years are shown in Figure 1. They are averages based on the number of set found during the entire summer on the inside surfaces of 100 shells at each station. As can be seen, during the 18-year period the oyster set was usually heavier than that of the starfish. The only exception was 1938 when the average seasonal starfish set per station was 1731 per 100 shell-surfaces, as compared with 1090 for the oysters. The year of maximum starfish set for the entire period of our observations was also 1938, while the year of heaviest oyster set was 1939 when 42,623 spat per station was the season's average. As the other extreme, we may mention that in 1945 only one recently-set starfish was found on our collectors during the entire summer, while the lightest oyster set occurred in 1943 when the average seasonal set was only 72 spat per station per 100 shell-surfaces.

To study further the discrepancies in the setting of the two species, product-moment correlations between the oyster and starfish sets were computed with the set for each year expressed as a percentage of that of the year when the highest setting took place. Thus, 1939 was taken as the 100 per cent year for oysters, and 1938, for starfish. This approach gave a range for each variable of 0 to 100 per cent. In each case, however, the distribution was badly skewed with most of the years falling between 0 and 10 per cent.

To make the analysis more detailed, correlations were determined for the stations located at each of three depths and also for the combinations of stations at several depths.

All correlations obtained were very low:

For 10-foot stations only	$r = .06$
For 20-foot stations only	$r = -.05$
For 30-foot stations only	$r = .03$
For 10- and 20-foot stations	$r = -.02$
For 10-, 20-, and 30-foot stations	$r = -.01$

With N, number of years in this case, being 18, the product-moment correlation (r) must be at least .47 to be significant at the .05 level. The low correlations obtained indicated that there was no definite relationship between the oyster and starfish sets. However, since the distribution of the data was badly skewed, we thought that the use of the conventional product-moment correlation coefficient might give somewhat misleading results. To verify the conclusions we decided to use rank-order correlations (r_s) also. For this, the yearly setting data of each species were assigned ranks from 1 to 18, in order of magnitude, and the correlations were then computed according to the rank correlation coefficient formula. The coefficients obtained were as follows:

For 10-foot stations only	$r_s = .19$
For 20-foot stations only	$r_s = .03$
For 30-foot stations only	$r_s = .06$
For 10- and 20-foot stations	$r_s = .07$
For 10-, 20-, and 30-foot stations	$r_s = .02$

Since the value of the rank-order correlation coefficient necessary for significance at the .05 level, with N = 18, is .47, all correlations obtained were not significant.

The absence of correlation was also well illustrated by scatter plots of the oyster set against the starfish set. A plot showing the lack of relationship between the rank-order of the set of the two species at the 10-, 20-, and 30-foot stations all combined in one group, is given in Figure 2. As may be seen from this plot, and from the low coefficients for each depth and combination of depths, almost complete dissociation is suggested between the variables. Therefore, we concluded that there is no appreciable relationship between the intensities of the starfish and oyster sets for the years and depth-stations for which data were available.

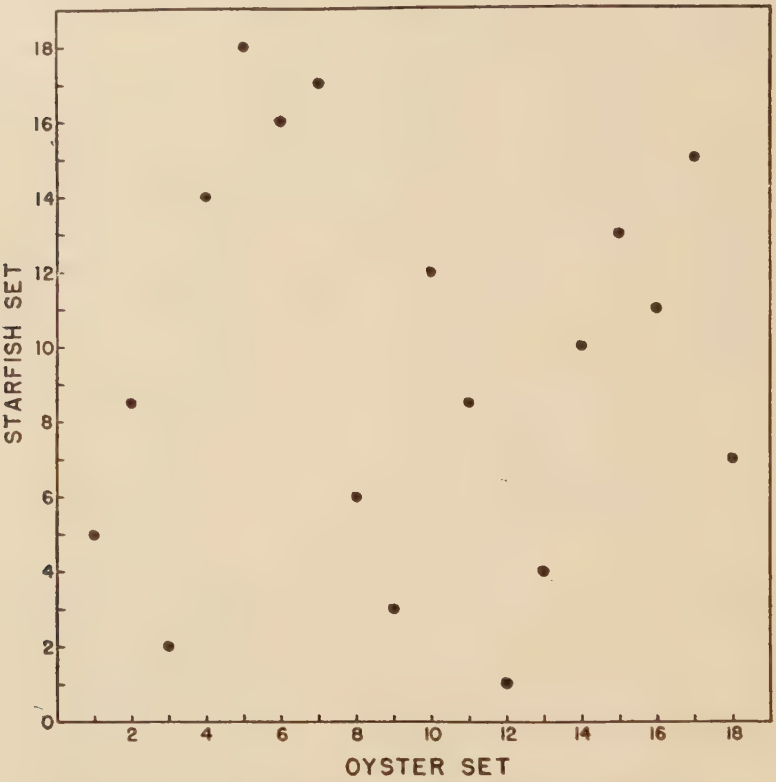

FIGURE 2. Rank-order relationship of oyster and starfish sets at 10-, 20-, and 30-foot stations. Long Island Sound, 1937–1954.

These studies, conducted for almost two decades, emphasize once more the danger of forming conclusions regarding the relationship between certain natural phenomena, if such conclusions are based on relatively short periods of observations. For example, if only the first four years of our period of observations were considered, a highly significant negative correlation between the intensity of the oyster and starfish setting would be indicated (Fig. 1). This, obviously, could lead to serious misconceptions. In our case, fortunately, by continuing the studies for many more years a much truer understanding of the situation was made possible.

The question naturally arises as to the causes responsible for the absence of a well-defined pattern in the intensity of setting of the two species in relation to each other. At present we are not prepared to discuss this question at length. Nevertheless, as mentioned above, we know that adult oysters and starfish live and propagate under the same ecological conditions, and that their larvae, which are present in the water during the same season, are subjected to the same general sets of environmental factors. We may suppose, therefore, that unfavorable conditions, such as relatively low summer temperature, strong winds, etc., would affect the larvae of both species more or less equally. Because oyster and starfish larvae are microscopic in size and both pelagic, we may also assume that most of the predators of one would also be feeding upon the other.

Low salinity, conversely, might be suspected as a factor which could unfavorably affect starfish larvae while leaving oyster larvae relatively unaffected. It is known that even adult starfish cannot survive in a salinity lower than 16.0 parts per thousand (Loosanoff, 1945), while oysters can normally live and reproduce in water of much lower salinity. However, in Long Island Sound proper, where our studies have been conducted, the salinity in summer is steadily near 27.0 parts per thousand, thus being within the optimum range for both starfish and oysters. Consequently, this ecological factor cannot be considered, under our conditions, as important in favoring one or the other species.

The density of the parent populations in different years is another factor to consider. Our observations on these populations (systematic surveys of the occurrence and distribution of starfish are made twice a year and oysters are collected near our stations at weekly intervals during the summer) showed that never during the period of our studies was the density of either population so reduced as to be below the minimal. In general, the starfish population of Long Island Sound remained large, as attested by our surveys and also by the extensive and continuous efforts of the oyster growers combatting these pests. The oysters, although reduced in number because of poor sets during the past seven or eight years, and the heavy mortality caused by the storm of 1950, are still numerous enough to be counted by the hundred thousand bushels. For example, we know that on the beds of a single oyster farming company in the Bridgeport area, there are now approximately 150,000 bushels of two-year-old oysters. Considering the unusually high fecundity of the oyster and the comparatively high fecundity of the starfish we believe that there are still sufficiently large parent populations of both species to produce enough spawn so that, under favorable conditions for survival and growth of larvae, heavy sets could result. This was well demonstrated for starfish during the summer of 1952 (Fig. 1). Since we know this and since our other studies, to be reported elsewhere, have shown that there is no direct relationship between the numbers of spawners available and the intensity of setting of oysters or starfish in Long Island Sound, we may conclude that the fluctuations in parent populations were not the principal causes responsible for the lack of relationship observed between the intensity of setting of the two species during our 18-year studies.

Although at this time we lack data to demonstrate it, an absence of relationship in the intensity of setting of oyster and starfish larvae may be due to only one or to a few causes of rather specific nature. For example, there is little doubt that the larvae of the two species may exhibit different food requirements, as far as size and quality of food organisms are concerned. Thorson (1946) says that an advanced echinoderm larva can take in particles as large as 50 μ, while our observations have shown that even "eyed" oyster larvae, about ready to metamorphose, require food of much smaller size, probably not over 15 μ in diameter. Moreover, since it has already been demonstrated that the larvae of even such closely related species as oysters and clams display widely different food requirements (Loosanoff, 1950; Davis, 1953), it is clear that even those food forms that are small enough to be taken in by both species may not be assimilated by one of them. Consequently, the presence or absence of such specific food organisms may be primarily responsible for the survival and, therefore, intensity of setting of larval oysters or starfish.

Another possibility to be considered is what we call, for lack of a better name, "water factor", which probably indicates the presence in sea water of certain dissolved substances that are needed for the normal existence and development of certain marine animals. These aspects of sea water chemistry and of animal behavior are still not well understood but we have evidence indicating that under laboratory conditions the presence or absence of this, at present, undetermined substance, or substances, may affect the growth of larvae of one species while not affecting the larvae of another closely related form (Davis, 1953).

Finally, only recently has the attention of biologists been called to diseases and parasites of lamellibranch larvae (Davis *et al.*, 1954; Loosanoff, 1954). It is possible, then, that larvae of other marine invertebrates, such as starfish, may also be victims of attack of different pathogenic micro-organisms, and that these micro-organisms may affect only closely related groups. If this is true, such organisms may sometimes eliminate the larval population of one species without harming the other. As a result, although most of the other conditions of the environment would be equally favorable to larvae of both forms, the larvae of the species suffering the epidemic would fail to set. Perhaps pathogens, together with specific food requirements of the larvae and the role of the water factor in their existence, explain in part the lack of relationship in the intensity of setting of oysters and starfish in Long Island Sound.

Since in the history of marine biology there are only a few studies when simultaneous systematic observations of the reproductive behavior of two ecologically closely associated species have been conducted steadily in the same area for long periods, we hope that the information offered in this article will contribute to a better understanding of the fluctuation in the natural populations of marine invertebrates existing in the same habitat.

We wish to extend our thanks to Barbara Myers for the statistical analysis of the data used in this article and to Rita Riccio for helping prepare the manuscript.

SUMMARY

1. No consistent relationship was found between the intensities of the oyster and starfish sets of Long Island Sound during the 18-year period, 1937-1954.

2. It is suggested that specific larval diseases, specific food requirements and presence or absence in the water of certain, at present, undetermined substances,

may be responsible, to a large extent, for the fluctuations in the intensity of setting of the two species in different years.

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GROWTH OF OYSTERS WITH DAMAGED SHELL-EDGES

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During the past few years several papers have appeared dealing with the structure and other characteristics of oyster shells. Medcof (1944) discussed the structure, deposition and quality of the shell of the American oyster, *Crassostrea virginica,* while Korringa (1951a, 1951b) described at length the structure of the shell of the European oyster, *Ostrea edulis,* and also considered it as a habitat harboring numerous species of the epifauna of oysters. Korringa also incorporated in his papers an extensive review of the literature on shells of other oysters and related mollusks. Owen (1953) commented on the shells of lamellibranchs but confined himself almost exclusively to the matter of shell form.

No systematic observations, however, had been made to determine whether damage to oyster shells, such as breaking off their edges, would result in a more rapid growth, which would partly or wholly compensate for the loss caused by the breakage. The present studies were undertaken because we thought that information on this subject would be of both biological and practical significance.

A review of the literature shows that only the articles of Glaser (1903, 1905a, 1905b) and Nelson (1921) discussed a subject related to our problem. Glaser found that mis-shaped oysters, *Ostrea virginica* (now *Crassostrea virginica*), which had grown under unfavorable, overcrowded conditions, would eventually attain normal shape if replanted with ample room for unobstructed shell-growth. He also found that oysters, the growth of which had been inhibited by physical obstruction, would show rapid growth of shell in the affected areas after the obstruction was removed. Nelson (1921) later came to the same conclusions.

Breaking of shell-edges is common when heavy dredges are used for gathering oysters, as is the practice in Long Island Sound and in many other areas where the oyster beds are located at a considerable depth. The damage is especially severe if the oysters are dredged during periods when the new shell-growth is still thin and brittle. In Long Island Sound the most rapid increase in the length of oysters takes place during May, June and July, representing, respectively, 22.57, 19.03 and 22.12 per cent of the total annual increment (Loosanoff and Nomejko, 1949). The oysters dredged during that period usually have a considerable part of the new shell-growth broken off. Since in some areas the oysters may be handled several times annually, and because each time many of them may have the edges broken off, the accumulated loss of shell may be quite significant.

Our first experiment was begun July 18, 1946. Fifty oysters were divided at random into two equal groups. The oysters of the first group, designated as the control, were measured to determine their length, representing the greatest anterior-posterior dimension (Table I). The oysters of the second group were measured in a similar way, but after the initial measurements had been made the edges of their shells were filed off.

TABLE I

Original mean length and increase in mean length of shells of normal oysters and of oysters the shell-edges of which were filed off. Milford Harbor, 1946, 1947 and 1949. Measurements in millimeters

Group	Original length	Length after filing	Decrement due to filing	Length at end of season	Increase over		Per cent increase over	
					Original length	Filed length	Original length	Filed length
1946								
Control	69.5	—	—	91.7	22.2	—	31.9	—
Damaged	68.7	61.7	7.0	89.6	20.9	27.9	30.4	45.2
1947								
Control	92.7	—	—	102.9	10.2	—	11.0	—
Damaged	91.4	84.5	6.9	104.4	13.0	19.9	14.2	23.6
1949								
Control	85.4	—	—	112.8	27.4	—	32.1	—
Damaged	83.4	79.7	3.7	111.1	27.7	31.4	33.2	39.4

In filing, the shell material was removed all the way around the "bill" instead of only in one place, near its end (Fig. 1). The filing reduced the mean length of the shells by about 7.0 millimeters (Table I). The filed-off material consisted not only of recently-formed, thin and transparent shell but also of the thicker, old portion, some of which may have been formed the preceding year. After the filing the oysters were re-measured, and both groups were placed in wire trays, which were suspended side by side in Milford Harbor.

Since the filing was done by hand and slowly, the oysters had enough time to contract the edges of the mantle, avoiding injury to it. Because of this the amount of mantle tissue remained the same as before the filing, thus still possessing the original area of secretory surface for the formation of new shell.

For clarity of description, all the oysters, or groups of oysters, the shells of which were filed off in these experiments, will be called the damaged oysters, while the unfiled ones will be referred to as the control. The oysters used in these experiments were adults, three to six years old.

On December 6, 1946, when the water in Milford Harbor was already cold enough to stop shell-growth, the oysters were again examined. The measurements showed that during the period of the experiment the damaged oysters had added more new shell-growth than the controls. In general, since the date of filing, the mean length of the damaged oysters showed an increase of 27.9 mm., while that of the controls was only 22.2 mm.

The experiment was repeated again in the summer of 1947 using 50 individually-marked oysters for each group (Table I). The shells of one group were filed off on August 14, and then both the damaged and the control oysters were suspended together in the same tray in Milford Harbor. After the beginning of the hibernation period the oysters were again examined. It was found that, as indicated by the increase in length, the damaged oysters had not only added more new shell-growth than the controls, but had actually outgrown them by the end of the season.

In 1947 both groups of oysters grew less than those used in 1946. This can be attributed to several considerations: first, the 1947 experiment was begun approximately one month later than that of 1946. Secondly, the oysters used in 1947 were considerably larger than those used in 1946 and their rate of growth could be expected to be slower than that of the smaller and younger oysters (Loosanoff, 1947). Finally, since the locations of the trays in which the oysters were suspended varied in the different years, the oysters may have been subjected to a somewhat different set of ecological conditions.

The experiments conducted in 1946 and 1947 showed conclusively that the oysters, the shell-edges of which had been filed off, compensated for this loss by forming new shell at a more rapid rate than the uninjured oysters living under identical conditions. However, since the experiments of these two years were not initiated at the beginning but approximately in the middle of the growing period, the experiments were repeated once more, starting in the spring when the oysters come out of hibernation, and continuing until late fall when the water again becomes too cold for oysters to grow.

On April 14, 1949, two groups, each composed of 110 individually-marked oysters, were treated as described above, and suspended in trays. Because the experiment commenced at the beginning of the shell-growing period, which in our waters usually occurs during the second half of April, the parts of the shells that were filed off consisted exclusively of old shell material that had been formed the year before. The restoration of that portion of the shell could be considered, therefore, as a true regenerative activity on the part of the oysters.

Final examination and measurements of the oysters were made on October 27. Three oysters were found dead in the control group but none in the damaged one.

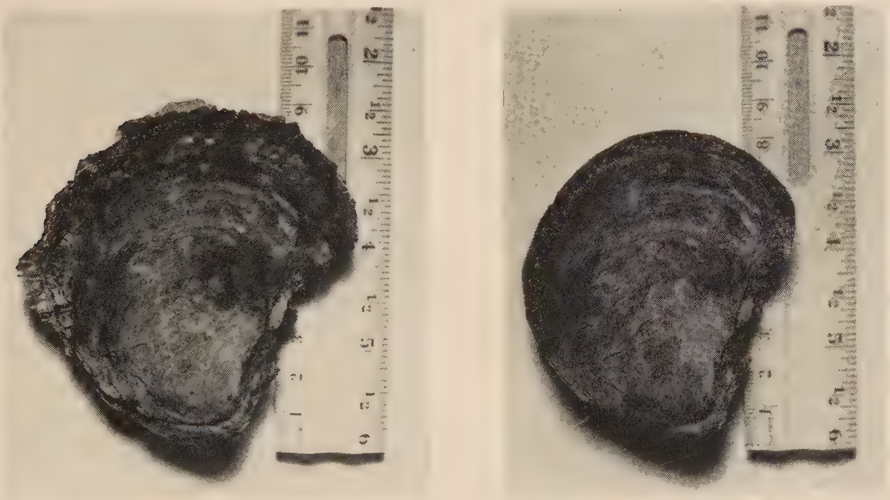

FIGURE 1. Photographs of the same oyster taken before and after the shell-edges were filed off.

The measurements showed that the damaged oysters again increased in length more than those of the control group (Table I).

Since the shell-edges of oysters may be broken off any time during the year, an experiment was devised to determine whether the tendency to compensate for such damages is present throughout the growing season, which extends from April to November (Loosanoff and Nomejko, 1949). The experiment was conducted as follows: On April 8, 1948 oysters that came from the same source were divided at random into five groups each containing 55 individuals, and the mean length of the oysters of each group was determined (Table II). The shells of Group 1, designated as the control, were not filed off during the entire period of observation. The shells of Group 2, however, were filed off on April 8, to provide information on the growth of oysters, the shells of which would be broken early in the spring, at the very beginning of the growing period. After filing, the oysters of Group 2 were again measured. All five groups were then suspended in wire trays in Milford Harbor, presumably under identical conditions.

As the season progressed, the oysters of Groups 3, 4 and 5 had their shells filed off. Each time measurements were taken before and after filing (Table II). Group 3 was filed off on July 13, Group 4 on August 9 and Group 5 on September 7. Thus, the entire season was roughly divided into four periods. Each time a group had its shells filed off and the length recorded, the length of the control group was also measured.

During this experiment 46 oysters were either lost overboard, died, or had their shells broken accidentally, thus becoming ineligible for further observations. The loss was especially serious in our control group when approximately half of it was lost near the end of the experiment. Nevertheless, 229 oysters were still available and our statistical analysis was based on these individuals. The number of oysters remaining in each group was as follows: Group 1—26; Group 2—54; Group 3—54; Group 4—51; and Group 5—44.

TABLE II

Original mean length of five groups of oysters and increase in mean length of normal oysters and of the oysters the shell-edges of which were filed off during different months of the growing period. Milford Harbor, 1948. Measurements in millimeters

Date	Groups				
	1	2	3	4	5
April 8, 1948	88.01	84.26* 81.70**	84.41	82.14	82.42
July 13, 1948	96.95	—	95.56* 90.68**	—	—
August 9, 1948	101.61	—	—	96.01* 91.79**	—
September 7, 1948	106.87	—	—	—	104.19* 99.26**
November 29, 1948	114.61	110.83	113.09	109.16	110.68

* Measurements before filing.
** Measurements after filing.

TABLE III

Decrements and increments of mean length of shells of normal oysters and of the oysters the shell-edges of which were filed off during different months of the growing period. Milford Harbor, 1948. Measurements in millimeters

Aspects studied	Groups				
	1	2	3	4	5
Decrement due to filing	—	2.56	4.88	4.22	4.93
Actual Length Increment (final length less initial length)	26.60	26.57	28.68	27.02	28.26
Per Cent Actual Length Increment	30.22	31.53	33.98	32.90	34.29
Total Length Increment (Actual Length Increment plus decrement due to filing of edges)	26.60	29.13	33.56	31.24	33.19
Per Cent Total Length Increment	30.22	34.57	39.76	38.03	40.27
Increase in length since filing, in millimeters	—	29.13	22.41	17.37	11.42
Corresponding increase of control, in millimeters	—	26.60	17.66	13.00	7.74
Per cent increase in length since filing	—	35.65	24.71	18.92	11.51
Corresponding per cent increase of control	—	30.22	18.22	12.79	7.24

Regardless of the supposedly random sorting of the oysters at the beginning of the experiment into five groups we found later that the control, Group 1, had a somewhat higher mean length than the other four groups (Table II). Analysis of variance showed that the differences in the initial length were significant beyond the .05 level. Therefore, to avoid in the analysis difficulties that would result from a disparity in the initial length, we decided to base the analysis of the amount of growth, shown by the different groups throughout the entire period of the experiment, not on the final length but on the difference between the initial and final lengths. This difference was termed the Actual Length Increment (Table III).

The analysis of variance, to test for homogeneity of the five groups on the basis of their Actual Length Increments, showed no significant difference among the groups. The conclusion was formed, therefore, that by the end of the growing period the damaged oysters showed approximately the same length increment as would have been expected of them if their shells had not been filed off. It should be remembered, however, that the Actual Length Increment does not include the increment needed to make up for the loss in length due to filing of the shells. If these two increments were combined to form the Total Length Increment (Table III), this would clearly show that all the damaged groups of oysters added more new shell and consequently must have increased in length faster during certain intervals than the control.

The stimulation caused by filing of the shells did not induce a significant increase in length beyond that of the oysters in the control group. The observations showed that, regardless of when during the growing period the edges of the shells were filed off, the oysters grew just enough to compensate for this loss and then added to it the normally expected length increment.

Another measure considered in connection with our data was the Total Length Increment which, as already mentioned, consisted of the Actual Length Increment plus the decrement due to filing of the shells (Table III). (For the control group, obviously, the Actual Length Increment and the Total Length Increment were identical.) The analysis of variance for the four damaged groups on the Total Length Increment indicated that there were significant differences among the groups. This was especially true for Group 2 which showed a smaller Total Length Increment than the other damaged groups. However, this was to be expected because the decrement due to filing varied from group to group. Thus, the oysters of Group 2, which were filed earliest in the growth period, had the smallest decrement and, therefore, had to grow less in total length to achieve the same final length as the oysters of the other groups (Tables II and III).

It was thought that there might be a definite relationship between the amount of shell removed and the final length reached. However, it was established that the amount of damage, within our experimental scope, was not an important factor, that is, regardless of how great or slight the damage was, the individual oysters appeared to be stimulated only to the extent of compensating for the loss in length and then adding whatever additional increment would be expected under normal conditions. In other words, by breaking off more shell along the edges, the oysters could not be induced to reach proportionately greater length by the end of the growing season.

Although the experiments showed that breaking of shell-edges induces oysters to grow faster in length, we had no information concerning the rate at which such an increase proceeded. Because we had made no measurements on the oysters of Groups 2–4 after their shells had been filed, except the final one at the end of the growing period, there were no data for ascertaining the shape of the growth curve after the damage to the shells. It was thought, nevertheless, that since the damaged oysters showed practically the same Actual Length Increment as the control, the stimulating effect of shell-damage did not induce the oysters to grow at an accelerated rate throughout the remainder of the growing period. This was well illustrated by the oysters of Group 2, the shells of which were injured at the beginning of the growth period. This group, subsequently, had approximately eight months in which to grow at the accelerated rate if such rate were a reality. Nevertheless, the Actual Length Increment of these oysters not only did not exceed those of the three other damaged groups, but their Total Length Increment was the smallest (Table III).

Theoretically, there were at least two hypotheses regarding the rate of growth of oysters after damage to their shells. First, it could be assumed that following shell-damage the growth would continue at a somewhat accelerated but, nevertheless, even rate throughout the entire remaining portion of the growing period. The second possibility was that immediately after the damage the growth would proceed at a rapid rate but then, after sufficient growth had been added to the shell-edges to compensate for the original loss, the growth would decrease to the normal rate corresponding to that of the undamaged oysters. We thought the latter hypothesis was more probable because Group 5, which was damaged late in the growing period, still came up to parity with the other groups in the length increment, thus indicating very rapid growth within a short period. However, to solve this matter definitely we carried on the following experiment:

Two groups of oysters were selected from a common source on May 21, 1954. The average length and width of the oysters of both groups were identical, being 80.6 and 64.5 mm., respectively. After that the shells of one group were filed off, reducing the average length to 77.0 mm. and average width to 60.0 mm. Both groups were then kept under the same conditions. A week later the average length and width of the control oysters were 81.0 and 65.0 mm., respectively, while similar dimensions of the damaged oysters were 79.5 and 62.5 mm. After two weeks the length and width of both groups became identical, being 82.0 and 66.5 mm., respectively, thus indicating that during this short period the oysters with filed shells had caught up with the control oysters. From then on the oysters of the two groups grew at approximately the same rate, showing no significant differences. This experiment has proven, therefore, that the second hypothesis was correct, namely, that in injured oysters the growth proceeds at a rapid rate for a brief period immediately after damage and then decreases.

The rapid growth of the new shell, representing "repair" or regeneration of the portion of the old one removed by filing, is probably due chiefly to the fact that the mantle of the oyster can now protrude farther along the edges of the shell. Because of this the secretory activities of the mantle involved in the formation of the edges of the shell are accelerated. The accelerated growth continues until the shell has grown enough to establish the normal ratio between the size of the oyster body and the length and width of the shell. After that the increase in length continues at approximately the same rate as in the undamaged oysters.

A rapid "repair" of the edges of shells is possible only if the oyster itself, especially its mantle, remains uninjured. If the mantle is injured, the oysters may not be able to show any increase in length until they recover. We have observed a number of such cases under laboratory conditions and also in nature. The best example of the latter was the condition of the Long Island Sound oysters following the extremely severe and prolonged storm of November, 1950. During this storm the oysters were rolled on the bottom by the wave action for many hours and with such force that the shell surfaces acquired almost a polished appearance, while the edges of the shells were rubbed off to such an extent that often the soft parts of the oysters protruded between them. Many oysters died because of injuries, which usually involved the mantle tissue. Those that survived did not resume normal growth but developed into stunted oysters with thick, irregular shells. Oysters of this type are still found in Long Island Sound four years after the storm.

The observations discussed in this paper are concerned almost exclusively with growth of shells as indicated by length measurements. They do not cover other aspects of growth and we know that it is possible that while in some of our experiments the new, thin shell-growth indicated an increase in length, the weight and volume of the oysters may have been smaller than before the shells were filed. Nevertheless, our auxiliary experiments, designed to ascertain the rate of growth immediately after filing, showed that after the edges of the shells had been filed, as shown in Figure 1, the growth in width proceeded at the same rate as the growth in length. This suggests that breakage of shell-edges is repaired by growth of the same pattern regardless whether it is length or width that is involved in the damage.

Our studies represent only initial steps toward understanding various aspects of the growth of damaged oyster shells. The next experiment, which suggests itself, should consist of studying the growth of oysters, the shell-edges of which were broken several times during the growing period. The growth curve of repeatedly damaged oysters should differ considerably from that of normal oysters, or of oysters the shell-edges of which were broken only once during the season.

Another aspect of these studies could be directed toward ascertaining whether the growth of oysters of different ages and sizes, damaged in the same manner, would differ significantly from that of the oysters on which the present conclusions are based. Because we already know that during the first years the increases in length, width and depth of an oyster proceed at different rates than later in life (Loosanoff, 1947), we may assume such a difference to exist. This assumption would be in agreement with the observations of Glaser (1905b) who found that the recuperative power of overcrowded, mis-shaped oysters varies with age, young individuals recovering their normal shape more rapidly than old ones.

We wish to extend our sincere thanks to Barbara J. Myers for the statistical treatment of the data used in this article and to Miss Rita Riccio for her help in preparing and editing the manuscript. Our thanks are also due to several friends, especially Drs. T. C. Nelson and J. C. Medcof, who offered suggestions and advice.

Summary

1. These experiments, based on length measurements, showed that oysters, the shell-edges of which were broken off, compensate for this loss by forming new shell at a more rapid rate than undamaged oysters living under identical conditions.

2. Damage to shells does not stimulate oysters to grow at an accelerated rate throughout the remainder of the growing period. Immediately after the damage they grow rapidly to compensate for the loss and then continue to grow at the usual rate to add to their length the normally expected annual increment. Thus, no relationship was found between the amount of shell removed and the final length reached.

3. The ability of oysters to repair broken shell-edges and still grow to about the same length as undamaged oysters remains the same regardless of when during the growing season (April 8–September 7) the shells are broken.

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CONSTRUCTION DETAILS OF IMPROVED TUNA LONG-LINE GEAR USED BY PACIFIC OCEANIC FISHERY INVESTIGATIONS

By Herbert J. Mann*

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This report is a description of the latest type of fiber long-line gear now being used by Pacific Oceanic Fishery Investigations (POFI) to capture tunas in the central Pacific. It is a revision of an earlier report (Niska 1953) and contains a complete description of the gear and its use, with particular attention to changes made since the earlier report was issued.

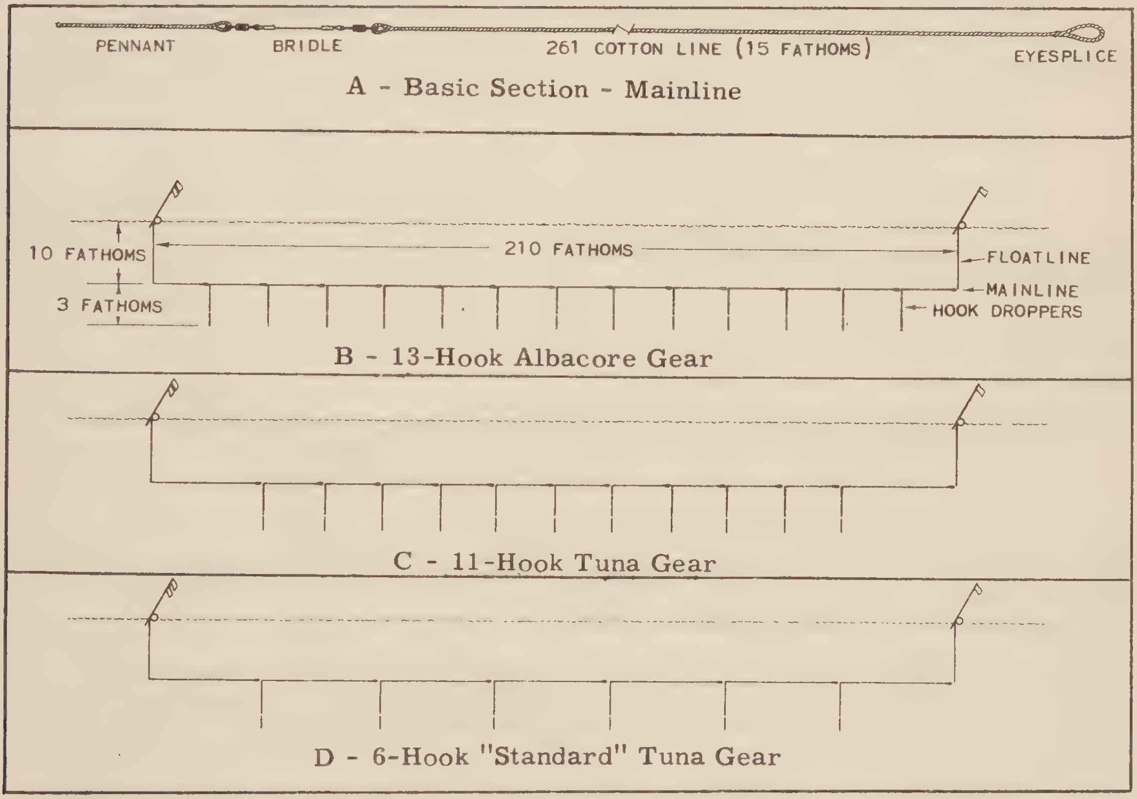
PENNANT
BRIDLE
261 COTTON LINE (15 FATHOMS)
EYESPLICE
A - Basic Section - Mainline
10 FATHOMS
210 FATHOMS
FLOATLINE
MAINLINE
3 FATHOMS
HOOK DROPPERS
B - 13-Hook Albacore Gear
C - 11-Hook Tuna Gear
D - 6-Hook "Standard" Tuna Gear

Fig. 1 - Three types of POFI long-line gear, and the basic component of their mainlines. A - 15-fathom section used in making up mainlines. B - 13-hook basket (unit) designed for albacore fishing. C - 11-hook basket used in fishing for larger tunas, such as yellowfin and big-eyed tuna. D - 6-hook "Standard" basket used in most of POFI's experimental fishing.

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The original POFI tuna long-line gear was derived from designs employed by Japanese and Hawaiian fishermen. A general discussion of the history, fabrication, and operation of such gear is included in reports by Shapiro (1950), June (1950), Murphy and Shomura (1953), and Niska (1953). So many changes have been made in the design of the gear since 1953 that a new account is necessary to acquaint the fishing industry with the successful innovations. It should be noted that the dimensions and basic design of the gear have not been changed; however, several modifications have increased the speed of setting and hauling and have resulted in greater flexibility. Each of these changes has been tested in the field under controlled conditions. The results of these field tests are discussed in Murphy and Shomura (1953), and Shomura and Murphy.[1]

GENERAL DESCRIPTION

The basic unit of the long line is the "basket" or "skate" (fig. 1), a 210-fathom length of mainline with droppers and buoyline, stored in a canvas skid or a bamboo basket. In the POFI experimental fishing operations about 60 such baskets are joined together to make a day's set. Since they are identical in design, plans of only one basket are shown in the diagram.

MAINLINE: The mainline of each basket is made up of 14 similar sections, each consisting of a 15-fathom length of cotton line with wire bridle and a short pennant or "pigtail" (fig. 1A). These sections are knotted together using the double sheet bend shown in figure 2. The principal advantage of such a system is that, since each section bears a one-hook dropper, various numbers of hooks from 1 to 13 per basket can be fished without resplicing or reworking the mainline. Another advantage of joining the sections with knots is that tangled sections of mainline may be removed without delay and set aside as the gear comes aboard.

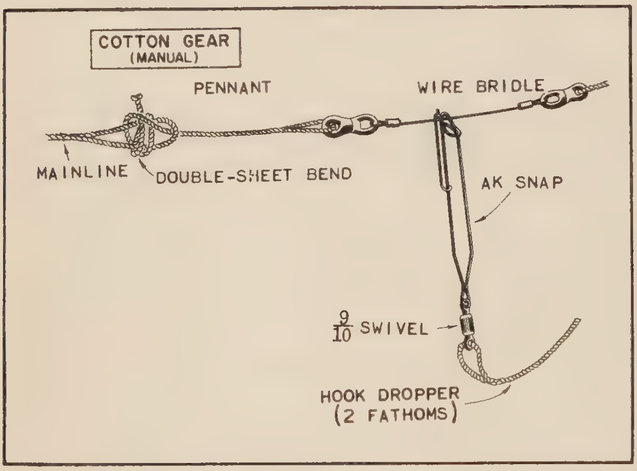

Fig. 2 - Method of joining two mainline sections, and details of wire bridle and branch-line attachment.

DROPPER ATTACHMENT: Each basic mainline section has a swiveled wire bridle for the attachment of droppers (fig. 2). This fitting has eliminated one of the most troublesome defects of the old gear. Formerly, mainline sections were made up with eyesplices at each end and were joined by knotting the loops together; droppers were attached by clipping an AK snap into one eyesplice. When the gear was hauled, the incoming mainline rotated because of the twist developed by the lay of the line and droppers were wound around it. The resulting tangles seriously delayed recovery of the gear.

The wire-bridle system has virtually eliminated this type of tangling. Droppers are now joined to the mainline by clipping the AK snap over the wire bridle. Since there is ample clearance between wire and snap, the mainline can rotate freely without affecting the dropper. The swivels at the ends of the bridle also help to reduce the twisting effect caused by the lay of the line.

HOOK DROPPERS: The 10-fathom and 5-fathom hook droppers, or branch lines (gangions), have been cut to 3 fathoms (over-all length, including leader) and the costly sekiyama[2] has been eliminated as unnecessary. The 3-fathom length marks the shortest length that can be efficiently fished; 2-fathom droppers have been tried but proved harder to coil and were more hazardous in setting and hauling than the 3-fathom type. Construction of droppers is shown in figures 2 and 3.

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[1] Long-line fishing for deep-swimming tunas in the central Pacific, 1953. U. S. Fish and Wildlife Service, Spec. Sci. Rep.: Fish. No. 157.

FLOATLINES: Floatlines, which join buoys and mainline, are made up of 5-fathom sections. The sections have an eyesplice at one end so that they may be joined by a double sheet bend. The depth of the mainline is varied by adding or removing sections without cutting or splicing line. Floatlines are joined to the mainline by the AK snap and knot shown in figure 4. Attempts have been made to use a wire bridle similar to the one used for the attachment for hook droppers, but the snaps opened up and this arrangement was discarded.

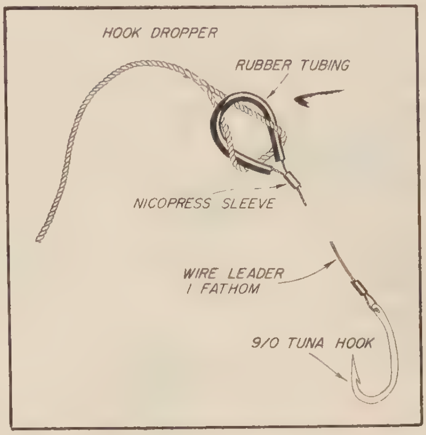

Fig. 3 - Details of branch line, leader, and hook assembly.

BUOY LIGHTS: Hauling operations may sometimes last until after dark, so battery-powered buoy lights are usually attached to the end poles and to several intermediate poles of the set. A typical light installation is shown in figure 5.

LONG-LINE CONTAINER: POFI long-line gear was originally stored in the standard bamboo basket commonly used in the Hawaiian and Japanese fisheries. This method of stowage was objectionable because of the space taken up by the empty baskets. POFI now stores gear in canvas skids similar to those used in the halibut long-line fishery (fig. 6).

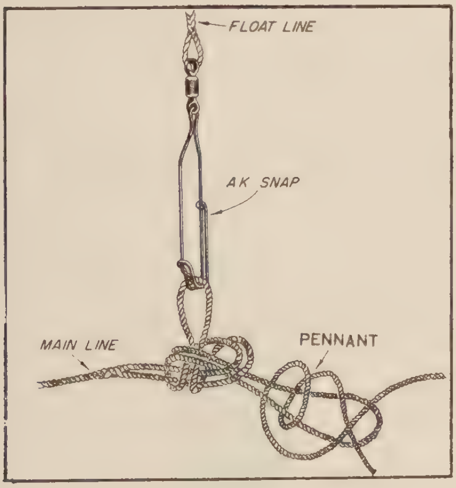

Fig. 4 - Attachment of floatline to mainline at juncture of two skates.

FABRICATION OF THE GEAR

PREPARATION OF LINE: Mainline, floatlines, and hook droppers are made of best grade hard-laid 261-thread cotton twine. Since the gear remains wet for long periods at sea, the line must be treated with some type of preservative. A commercial copper-base preservative is commonly used by POFI. Skeins of new line are cold-dipped for a period of three minutes in a full-strength solution and are then dried in the shade.

The treated line is then stretched and cut into 15-fathom lengths. To save time, several lines are cut simultaneously in the following fashion: skeins are opened out and placed on vertical reels; the ends of several lines are attached by brass swivels to the rear bumper of a jeep so that the lines can rotate freely to remove kinks; the lines are then unreeled and stretched out over a measured 15-fathom distance and a steady strain of 125 pounds is exerted until kinks are eliminated. A Dillion dynamometer is used to check tension on the lines and prevent overstretching.

MAINLINE: Cut lines are coiled down in sets of 14 pieces each, the number required to make up one skate. These basic mainline sections are then completed by splicing in eyes, wire bridles, and pennants as shown in the diagram (fig. 1A). The end pennant of each basket is made from $\frac{1}{4}$-inch cotton rope rather than 261-thread line and the end eyesplice is lengthened.

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[2] Sekiyama or shanawa--a stiff pennant consisting of a linen or wire core served with cotton twine, used by Japanese and Hawaiian fishermen to connect the wire leader to the cotton branch line, and formerly employed in POFI long-lines.

Wire bridles 6 inches long are fashioned from $\frac{5}{64}$-inch 1 x 7 stainless wire rope. No. 2 Seadog swivels are fastened to the wire by means of Nicopress fittings (fig. 2).

HOOK DROPPERS: The construction of hook droppers is shown in figures 2 and 3. Two-fathom lengths of treated 261-thread line are made up with a special snap at the upper end. This snap, a model used by the Northwest trolling boats, is a No. 9/0 Kolstrand AK snap, but is constructed of heavy No. 7 wire and has a jaw opening of $\frac{1}{8}$-inch diameter. It is important that the AK snap be designed to fit the wire bridle with a small clearance, since otherwise the snap is apt to jam against the swivel. The lower end of the dropper terminates in an eyesplice to which is joined hook and leader, as shown in figure 3.

The leaders are fashioned of 6-foot lengths of .066-inch diameter right lay 1 x 7 galvanized plow-steel wire. Galvanized wire is used rather than stainless steel since it reduces the electrolytic action between hook and leader. Stainless steel leaders destroy hook plating in a very short time. A 3-inch loop in the end of the leader is fitted with a section of $\frac{3}{8}$-inch O.D. x $\frac{1}{8}$-inch I.D. industrial rubber tubing, which serves to prevent chafe. A 9/0 or 8/0 tuna hook is attached to the leader by a 1-inch loop fastened with a Nicopress sleeve (fig. 3). It should be noted that the hook is of a special shape, with a bent shank which allows the bait to hang in line with the leader. Such a hook has better fish-holding qualities than the conventional straight-shanked models.

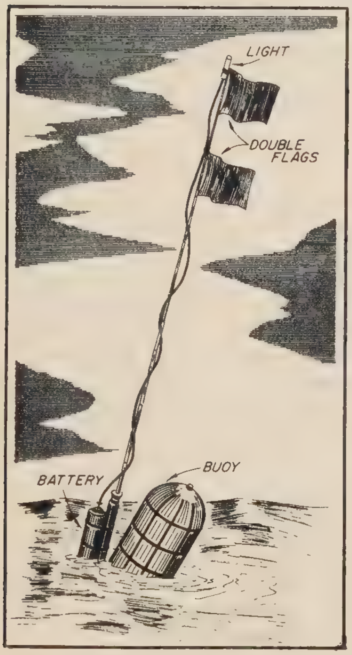

Fig. 5 - Battery-powered light buoy.

FLOATLINES: Floatlines are made from 5-fathom lengths of 261-thread line. An AK snap is spliced into one end and an eye formed in the other. Mainline and floatlines are joined as shown in figure 4.

FLOATS: Floats used in the Hawaiian fishing industry include glass balls, wood billets, and metal tanks of various sizes. The floats used by POFI are made from surplus stainless-steel oxygen tanks of 2,100 cubic inches internal volume (figs. 7 and 8). These are fitted with a $\frac{3}{8}$-inch galvanized eye bolt for attachment of a floatline. Since the tank comes provided with a $\frac{1}{4}$-inch outlet, it is necessary to reduce this opening by fitting a $\frac{1}{8}$-inch to $\frac{1}{4}$-inch hexhead pipe bushing between tank and bolt. An 8-inch grommet of $\frac{3}{8}$-inch diameter manila rope is spliced into the eye for attachment of the bamboo pole. A $\frac{3}{8}$-inch stainless-steel thimble protects the grommet against chafe (fig. 8). Buoys are painted a bright orange for greater visibility.

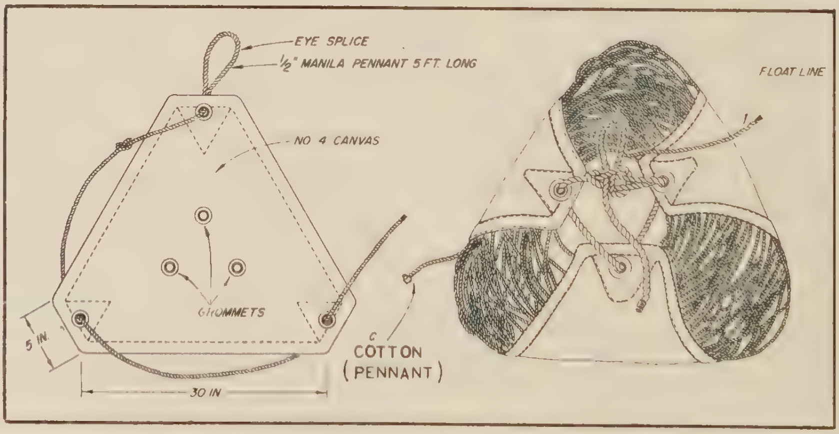

Fig. 6 - Canvas skid for stowing long-line skates.

FLAGPOLES: Alternate buoys have poles with flags to serve as markers in locating gear (fig. 7). Poles are select bamboo 14 to 16 feet in length with a butt diameter of $1\frac{1}{4}$ inches to $1\frac{1}{2}$ inches and a tip diameter of about $\frac{5}{8}$-inch.

The poles are protected from chafing on the floats by a 15-inch section of heavy air hose. Split lengths of hose are clamped on the pole with a lower end 6 feet 6 inches from the butt. Clamps are $\frac{3}{8}$-inch Band-It straps secured with the buckles fixed over the cut. This attachment is made so that the buckles are turned away from the buoy, presenting only the smooth band to minimize chafing.

A 5-inch loop of $\frac{3}{8}$-inch manila line is fastened at the bottom of the pole for attaching the floatline. This loop is held in place as follows: a rosette is made in each end of the line and a Band-It strap is clamped midway on the rosette, which serves as a cushion preventing the loop from slipping under the band. The ridge at the lower joint of the pole tends to prevent the loop and band from slipping off the butt of the flagpole.

The float is tied to the flagpole by a 4-foot lanyard of $\frac{3}{8}$-inch manila line, which is secured to the flagpole just below the chafing gear. The end of the lanyard next to the pole ends in an eyesplice, as shown in figure 8. A safety line of 261-thread cotton line runs from this eye to the bottom of the pole, where it is made fast to the manila loop. If the bamboo pole breaks during fishing operations, the safety line prevents loss of buoy and floatline. On setting the gear, the free end of the lanyard is joined to the grommet of the float by a reverse sheet bend with bow (fig. 8).

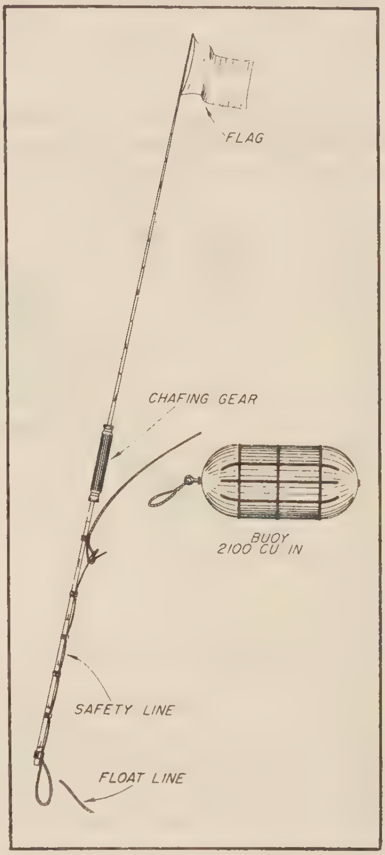

Fig. 7 - Complete flag and float assembly, showing chafing gear.

Bunting flags are attached to the top of the flagpoles by waxed, doubled, cotton-thread ties fixed to the corners of the flags. POFI flags are dyed a bright orange since this color seems to show up well under all sea conditions. The size of flags has been increased to $1\frac{1}{2}$ square feet in an effort to increase the range of visibility. Double flags are used to mark various portions of the set such as the ends and center.

CANVAS SKID: To make the skid (fig. 6), No. 4 canvas duck is cut in the shape of an equilateral triangle 45 inches on a side. Corners are turned in with No. 5 grommets punched in the center. A $\frac{3}{8}$-inch manila becket, 60 inches long, is laced through the grommets. A 3-inch loop is spliced on one end, and the standing end is securely whipped. The loop is secured on one grommet by an overhand knot immediately behind the eyesplice. With the line in place the standing end is laced through the other two grommets and passed through the eye to form a bight. A slip knot finally secures the line. Skids have brass grommets in the bottom to provide proper drainage and ventilation of wet line.

ASSEMBLING LINES FOR SETTING

Prior to setting, mainline and branch lines are assembled and the gear is carefully coiled down on the skid. The bottom end pennant is left exposed for joining to the next basket (fig. 6). Hook-dropper coils are made up smaller than mainline coils and are secured by hooking the tuna hook into the rubber chafing gear on the wire leader. The floatline is coiled down on top of the pile, the skid is then tied up, and the gear is ready for setting.

SETTING

The gear is laid in a straight line and in a direction relative to the wind and sea which will make it easy to haul the line. Hauling is easiest when the wind blows from about 30° off the bow on the side of the line hauler. Therefore, gear is usually laid with the wind about 30° off the stern opposite from the line hauler. When course is reversed to pick up the gear, if no wind shift has occurred, the winch side will be the weather side and wind and sea will be broad on the bow.

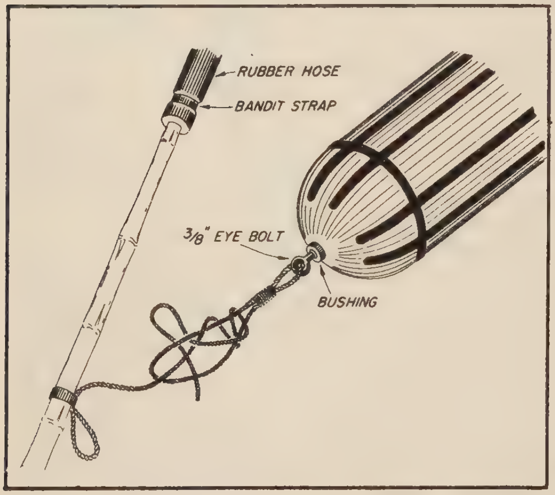

Fig. 3 - Details of attachment of float to flagpole.

When setting close to islands or banks, or in an area where currents are known to be strong, the direction of set must be chosen with care. Setting across a current boundary is avoided as the mainline is apt to part with the strain. Particular care must be taken in setting in shoal water close to land where strong surface currents may sweep the gear into shallow water before it can be recovered.

Setting is usually done from a "setting table" on the stern of the vessel. This is a wooden bench large enough to hold several skates of gear and the bait needed for the set. In setting (1) the vessel is put on the desired course; (2) floatline, buoy, and flagpole (usually with double flag) are joined to the first basket and pitched overboard; (3) one fisherman pays out coils of mainline while others uncoil droppers and bait hooks.

The amount of slack in the mainline, and consequently the fishing depth of the gear, is controlled by the fisherman throwing out the mainline coils. These may be thrown out rapidly to give a "slack set" which fishes at a comparatively great depth, or they may be held until the line is stretched out taut by the vessel, which results in a comparatively shallow fishing depth. A slack set may also be accomplished by steering a zigzag course while paying out the line.

HAULING

LONG-LINE HAULER: The gear is hauled with a Japanese line hauler of the type shown in figure 9. Such a winch is used in preference to an ordinary gurdy because it coils down the mainline automatically with little attention from the winch operator.

The coiling of the line is accomplished by the hauling head shown at the top of the winch. This assembly consists of a split sheave (A) grooved to fit the diameter of the line to be hauled; a wide center wheel with replaceable rubber collar (B); and a movable brass idler (C) controlled by the lever at the left. All three units are connected by a gear train which synchronizes them when they are turned by the drive shaft in the base of the winch.

In hauling, the incoming line is led under the grooved sheave, then over the center wheel and between it and the brass idler. The grooved sheave grips the line and the idler squeezes it against the rubber collar giving friction to pull the line in as the sheaves rotate.

The line is deflected downward by the brass plate (D) to a platform below, where it coils itself. The size of the coil is dependent upon the distance between plate and platform, so it is necessary to adjust the height of the latter with care.

The hauling head is turned by the drive shaft at the bottom of the winch through a multiplate oil-bathed disc clutch located in the base of the winch. The foot-operated clutch control is mounted near the ship's bulwark close to the overside roller so that the winch operator can see the incoming branch lines easily. The clutch control is so arranged that the winch operates continuously unless the clutch pedal is depressed.

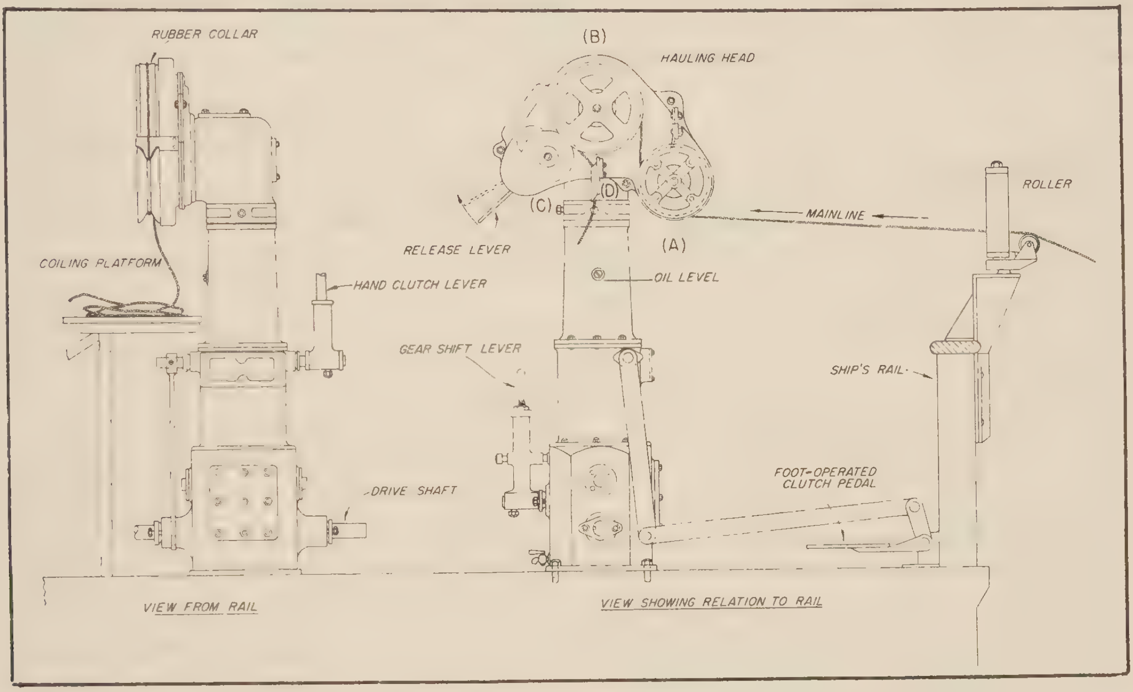

Fig. 9 - Japanese long-line hauler.

The gear-shift lever shown at the lower left controls the hauling speed. With a drive shaft input speed of 300 r.p.m., high gear yields a line speed of about 1,000 ft./min., low gear a speed of 500 ft./min.

Hawaiian and Japanese fishing vessels frequently drive line haulers with a line shaft take-off from the main engine. On POFI vessels an electric drive (3 hp. waterproof motor d.c. 1,725 r.p.m.) and a 5:1 gear reduction, or a hydraulic drive (7.5 hp. 35.8 gal./min. pump at 1,200 r.p.m.) are used to power haulers.

HAULING PROCEDURE: Hauling operations on Japanese vessels have been described by Shapiro (1950) and Shimada (1951). On POFI vessels the mainline is brought aboard, led through the overside rollers, and fed into the line hauler. The winch is controlled by the clutch operator, who stands at the rail and stops the winch by the foot control to detach branch lines. The fisherman tending and coiling line can also stop the hauling by pulling back on the idler lever, thus releasing tension on the line. Floatlines and hook droppers are detached as they reach the overside roller. The buoys and flagpoles are untied and stowed, and the floatlines and droppers are coiled by hand. As the mainline coils under the line hauler, floatlines and droppers previously coiled by hand are reattached in the proper places so that the "basket" is ready for use the following day.

If the gear is not to be used for some time, as for example, when the vessel changes fishing grounds, droppers are removed from the mainline and are stowed separately. If practicable, hooks and leaders are removed from the droppers, for if assembled gear is stored wet for long periods, metallic components react with the damp line to cause weak spots. Gear is dried whenever possible, but exposure to direct sunlight is avoided.

MATERIALS USED TO MAKE UP GEAR

The following list of materials contains the items necessary to make up one basket of POFI 11-hook long-line gear. Prices of gear have been derived from Government bid quotations on material delivered in Honolulu and, because of fluctuations in market prices and shipping costs, are only estimates of cost to others.

Item	Quantity Required	Cost ($)
1. Mainline Section:		
Wire, stainless steel $\frac{5}{64}$" diameter 1 x 7, right lay	6 in.	0.03
Sleeves, Nicopress copper, $\frac{1}{16}$", 18-1-C	2 ea.	0.08
Swivels, brass, Seadog No. 2, trolling	2 ea.	0.46
Twine, cotton, 261-thread, treated	15 fathoms	1.25
Pennant, 261-thread twine, treated	24 in.	0.03
Total per unit		1.85
2. Floatline:		
Snap, AK, No. 9/0 design but made from 7/0 wire, brass barrel swivel	1 ea.	0.35
Twine, cotton 261-thread	10 fathoms	0.90
Total per unit		1.25
3. Float Assembly:		
Tank, surplus, stainless steel oxygen, 2,100 cu. in.	1 ea.	10.40
Eyebolt, $\frac{3}{8}$" x $4\frac{1}{2}$", galvanized	1 ea.	0.55
Bushing, pipe, $\frac{1}{4}$" - $\frac{1}{8}$", galvanized	1 ea.	0.16
Thimble, wire rope, $\frac{3}{8}$", galvanized	1 ea.	0.10
Manila rope, $\frac{3}{8}$" diameter	24 in.	0.05
Sealing compound, lashing twine	-	0.10
Paint, Westinghouse, orange enamel	$\frac{1}{2}$ pt.	0.40
Total per unit		11.76
4. Bamboo Pole Assembly:		
Pole, bamboo, 14' long x $1\frac{1}{2}$" at base	1 ea.	0.70
Flag, bunting, 14" x 18", orange	1 ea.	0.24
Hose, air, surplus, heavy	14 in.	0.80
Strapping, Band-It, $\frac{3}{8}$" width	18 in.	0.09
Buckles, Band-It, $\frac{3}{8}$" width	3 ea.	0.18
Rope, Manila, $\frac{3}{8}$" diameter	6 ft.	0.15
Total per unit		2.16
5. Hook Dropper:		
Snap, AK, 9/0 formed of 7/0 wire with brass barrel swivel	1 ea.	0.35
Twine, cotton, 261-thread	12 ft.	0.18
Tubing, rubber, black industrial, $\frac{3}{8}$" O.D. x $\frac{1}{8}$" I.D.	6 in.	0.08
Sleeves, Nicopress, $\frac{1}{16}$"	2 ea.	0.08
Wire rope, leader, .066" dia. 1 x 7 right lay plow steel, galvanized	6 ft.	0.06
Hook, 9/0 or 8/0 mustad flatted tinned, tuna	1 ea.	0.18
Total per unit		0.93

Item	Quantity Required	Cost ($)
6. Skid:		
Canvas, No. 4, triangle 45" each side	1 ea.	1.03
Manila rope, $\frac{1}{2}$" diameter	60 in.	0.20
Spur grommet, heavy, brass	6 ea.	0.12
Total per unit		1.35

Since POFI gear can be assembled so as to fish different numbers of hook droppers, the cost of individual baskets varies according to the type of gear used. Costs of typical gear assemblies are shown below:

Components	6-Hook "Standard"	11-Hook Tuna	13-Hook Albacore
Mainline--14 sections basket	$25.90	$25.90	$25.90
Floatline	1.25	1.25	1.25
Buoy.	11.76	11.76	11.76
Bamboo pole[1]	2.16	2.16	2.16
Droppers	5.58	10.23	12.09
Canvas skid	1.35	1.35	1.35
Total Skate	$48.00	$52.65	$54.51

[1] Bamboo poles are usually attached to alternate buoys only.

DISCUSSION

The greatest defect of the present gear is the relatively short life of the cotton twine used for mainline and droppers. Three factors combine to cause this relatively rapid deterioration

First, due to conditions inherent in the fishery, the line is often overstrained. This method of fishing is necessarily nonselective as far as catch is concerned, and large sharks and marlins often take the hooks. Heavy fish chafe the line and sometimes stretch gear beyond its elastic limit. Overstraining of the line also occurs during fishing operations in rough weather, for it is then difficult to keep the vessel close up to the gear. As the vessel drifts away from the set, the mainline is sometimes parted before the ship can recover position.

A second factor is wear and tear on the line during hauling operations. Some abrasion is due to chafing of hooked fish when droppers tangle with the mainline, but most of the damage is done by wear on the line as it passes over the rollers and through the line hauler. Wear is especially evident where swivels are inserted in the line.

Finally, the line deteriorates because proper care of the gear is extremely difficult. While on the fishing grounds, gear is set during the day and stored damp at night in the skids; it is frequently stored damp for several days at a time while the vessel changes fishing grounds. Under such conditions cotton line loses strength rapidly. It has been possible to make some progress in methods of preserving gear. For instance, POFI gear treated with copper-naphthenate preservatives now lasts about twice as long as the tan bark-treated line used in the Hawaiian fishery. Tarred line used exclusively by the industry in Japan and to some extent in Hawaii is now being tested but has not yet been evaluated.

It should be pointed out that the gear described in this report has not been designed primarily for commercial use. Rather, an effort has been made to develop a type of gear which would be extremely flexible and which could be changed rapidly for various types of experimental fishing. During the evolution of this gear, several design limits appear to have been reached. Thirteen hooks per basket appear to be the maximum number practicable with this type of gear. As many as 21 hooks per basket have been fished, but the net result was a slowing down and a reduction of efficiency in both setting and recovery of the gear. Hook droppers also have been shortened to their minimum length. Thus, it is anticipated that the general design of the gear may remain unchanged for some time but that futher improvements may well be made in the speed with which the gear is operated and the durability of the materials from which it is constructed.

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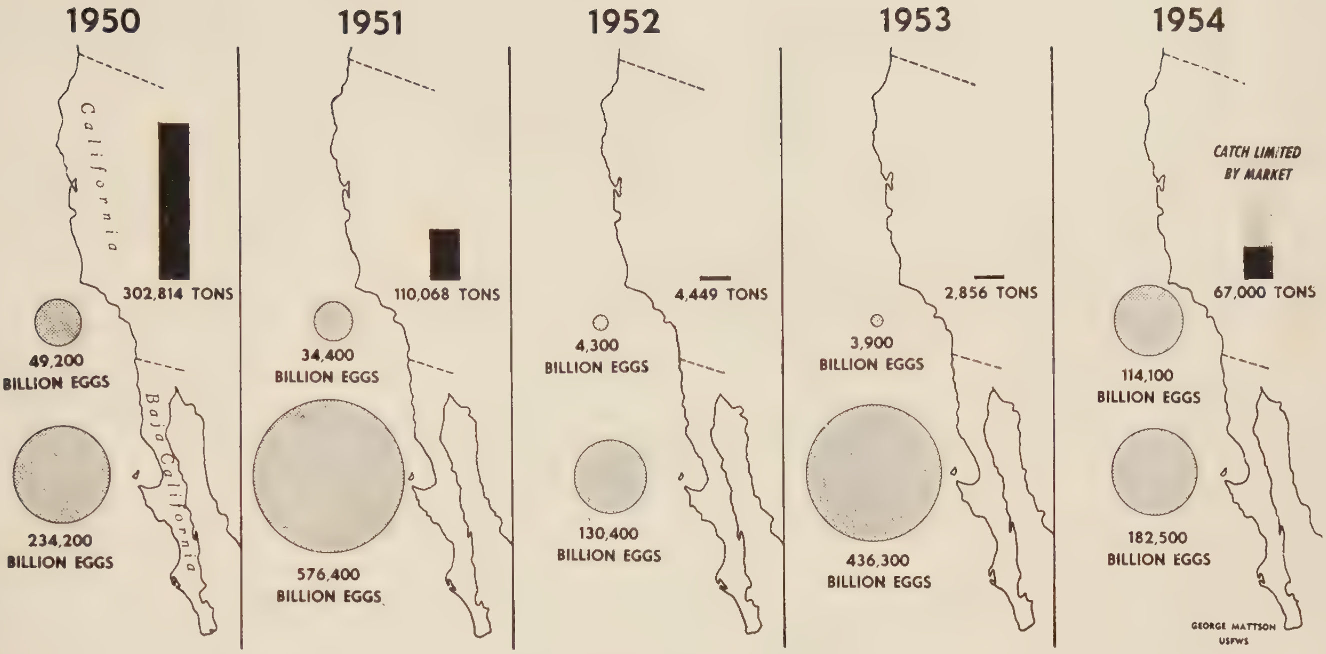

Abundance and distribution of sardine eggs in the spring months and the sardine landings at San Pedro in the fall and winter months. The areas of the circles are proportional to the numbers of eggs and the height of the bars are proportional to the tons landed at San Pedro.

SARDINE SPAWNING SURVEYS

By JOHN C. MARR

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FOLLOWING an exploratory series of cruises in 1949, the location and abundance of Pacific sardine eggs and larvae off the west coast of North America have been determined every year. These egg and larva surveys have been carried out by the South Pacific Fishery Investigations of the U.S. Fish and Wildlife Service as a major part of their work in the California Cooperative Oceanic Fisheries Investigations.

Cooperating agencies include the California Academy of Sciences, California Department of Fish and Game, Hopkins Marine Station of Stanford University and Scripps Institution of Oceanography of the University of California. Scripps and the Service have done the bulk of the oceanographic-biological work (excluding fish scouting cruises) as a joint operation.

Information from the egg and larvae surveys contributes to the solution of many problems. Outstanding among these are:

1. An estimate of the total number of eggs spawned each year provides a starting point in the survival curve of each year class. By observing the reduction in the numbers of larvae with time, it is possible to determine the stage at which mortality is most severe, to seek the causes of this mortality in the environment and thus to determine the cause of large variations in year-class sizes. (Large fluctuations in year-class size are characteristic of most of the great fisheries of the world and in general seem to be related not so much to the number of eggs spawned as to what happens to the eggs after they are are spawned.)

2. An estimate of the size of the spawning population of sardines may be obtained if the following are known: the total number of eggs spawned during the year, the total number spawned by each female and the ratio of males to females in the population.

3. The distribution of spawning fish can be determined from the distribution of eggs, since the eggs hatch in 2½ to 3½ days and cannot drift very far during this period. By no other method can the distribution of adult sardines at time of spawning be so completely described.

I wish particularly to discuss the information derived from (3) above and the application of this information.

A comparison of the distribution of spawning during the spring months with the catch landed at San Pedro in the fall and winter months is of interest. A "northern" spawning center lies off southern California and northern Baja California. A "southern" spawning center lies off central Baja California. In the accompanying figure the numbers of sardine eggs spawned in each of these areas in 1950 through 1954 are shown.

It is obvious that both in absolute numbers and percentage-wise, the number of eggs in the northern center decreased each year from 1950 through 1953. In fact, in 1952 and 1953 the amount of spawning in the northern center was almost negligible. However. in 1954 the amount of spawning in the northern center was the greatest observed in recent years. Compared to 1940 and 1941 (insofar as a comparison is possible—a much smaller [illegible] yed in

1940 and 1941), spawning in this center in 1954 was considerably less.

What causes these changes in the distribution of sardine spawning? Undoubtedly they are related, in part at least, to concurrent changes in the ocean. One feature of the environment that has been intensively investigated is temperature. It is known, for example, that the sardines which spawn in the spring months do so almost entirely in waters whose temperatures are between 55.4° F and 61.7° F. It is therefore suggestive, although by no means conclusive, to notice the association in time of changes in the distribution of sardine spawning (and adults, for that matter) with climatic changes.

Various sea surface and air temperature records show that the west coast of North America (U.S. and Canada) experienced a trend of increasingly warmer conditions from about 1910 to 1941. This trend was then reversed and was followed by increasingly cooler conditions until 1953. However, in 1954 and 1955 temperatures again rose. It is impossible to state whether the conditions in these last two years are merely deviations from the cooler trend, or if they presage the start of a new period of warming.

In addition to the distribution and abundance of spawning, the accompanying illustration also shows the sardine landings at San Pedro in the 1950-51 through 1954-55 seasons. For several reasons the catch at San Pedro in the fall does not vary in direct proportion to the number of fish spawning in the northern center in the preceding spring. It is interesting, however, that the two years of practically no catch were also the two years of practically no spawning in this area. This suggests that when fish are present on the northern center spawning grounds in the spring, they will also be present on the San Pedro fishing grounds in the fall.

The catch in the fall, however, will also be influenced by local peculiarities in fish distribution, possible movements off the fishing grounds and by economic demand. (The catch was probably considerably lower than it could have been in the 1954-55 season, owing to economic restrictions.)

The distribution and abundance of sardine eggs in the northern center in 1955 are comparable to what they were in 1954. Barring some unforeseen change in the movements of the fish, this suggests that the conditions for the 1955-56 season will approximate those of the 1954-55 season. ✶

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The Use of Morphometric Data in Systematic, Racial and Relative Growth Studies in Fishes[1]

JOHN C. MARR

MORPHOMETRIC data have, for obvious reasons, been employed widely in both the "old" and the "new" systematics, in the study of races or subpopulations of fishes and, somewhat more recently, in the study of the relative growth of body parts. The methods of handling such data have been far from uniform and, in addition, have led to the incomplete extraction of information from a given set of data or, in some instances, to erroneous conclusions.

In systematic studies, for example, body dimensions are usually expressed in per cent or per mille of standard length, often as averages (i.e., without respect to absolute standard length). Only rarely are the original measurements included. Even more rarely are regression techniques employed. When they are used, one is more apt to find the regression of "body part in per mille of standard length" on standard length than the regression of original variates. There are several possible reasons for these practices. One reason, and perhaps the main one, is merely historical precedent. A second reason is that often only one or a few specimens are available to the systematist and other methods are not appropriate. A third possible reason is that a lack of appreciation of variation and/or size-specific changes leads to the use of the convention. A fourth reason perhaps, is that even though a large series of specimens is at hand, the systematist may not be aware of the convenient methods which are available for treating morphometric data.

Racial or population studies based on body proportions are usually carried out by fishery biologists and, in general, are usually based on larger series of specimens than are conventional systematic works.[2] Racial studies generally, although not always, use the original variates and take advantage of the many conveniences of regression techniques.

Students of relative growth seem to have been the most progressive in the use of the appropriate statistical tools. One reason for this may lie in the fact that such workers have been interested not only in the manifestations of the relative growth of body parts, but also in the nature and causes of such growth.

Perusal of the literature and discussions with many interested individuals lead me to the conclusion that the wider use of regression analysis (of original measurements) would contribute materially to solution of the general types of problems mentioned above and, paradoxically, the use of such analysis (using ratios) has in the past led to confusing or doubtful conclusions. It is my hope that the following discussion will help to make the potential benefits evident, as well as to point out the various pitfalls to be avoided. It is my thesis

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[1] Published by permission of the Director, Fish and Wildlife Service, U. S. Department of the Interior.

[2] I distinguish between systematic and racial studies, not because of any inherent differences in the two, but rather because of the philosophical differences in approach to the problems. It seems a fair generality to state that the fishery biologist is inclined to realize that he is studying a dynamic situation in nature involving rather complicated sampling problems, whereas such inclination is apt to be much less pronounced in the systematist. Myers' (1952) comments are relevant.

(1) that the use of original measurements, rather than ratios, is time saving, easier to interpret, and less likely to lead to confusing conclusions and (2) that in the use of regression analysis of original measurements, the types of regression equations are not always used to best advantage, nor are their peculiarities fully appreciated.

Types of Regressions

The concept which makes regression techniques of value in morphometric studies is that the size or growth of one variable, say a body part, is related in a particular way to the size or growth of another variable, say the entire organism. If the form of the relationship and the size of the organism are known, it is possible to predict, within definable limits, the size of the body part. As a corollary, it is possible to distinguish individuals in which the relation of body part to organism exceeds the expected limits or takes a different form and which, therefore, must have been drawn from a different population with regard to this attribute.

Fortunately, it so happens that the relationship of part to whole may usually be represented by one or another of a few general equations. It also happens that, for those equations which are not rectilinear, it is often easy to make rectilinear transformations. Convenient methods have been worked out for characterizing and comparing rectilinear regressions and have been described in many statistical textbooks. (These methods have certain limitations in the case of small differences; see comments by Schaefer (1952).)

In discussing the various kinds of regressions, let us consider only the three forms to which the relationship of body part to body length most commonly conform.

The *rectilinear regression* may be expressed by

$$y = a + bx \ldots\ldots\ldots (1)$$

where y = the dependent variable (say length of body part); x = the independent variable (say body length); a (a constant) = the y-intercept or the value of y when $x = 0$; and b (a constant) = the slope of the line or the constant absolute change in y per unit change of x. Lines corresponding to (1) will always form a straight line on arithmetic coordinates.

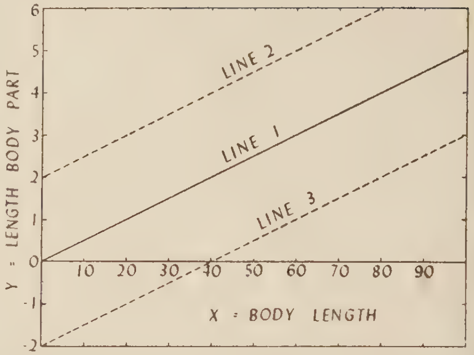

Fig. 1. Hypothetical examples of rectilinear regressions of the type $y = a + bx$.

An example of a rectilinear regression is given as line 1 in Fig. 1. Note that, in the example given, a unit change in x produces $\frac{1}{20}$ of a unit change in y, $b = .05$, and also that the line passes through the origin ($y = 0$, $x = 0$), $a = 0$. The equation for this line may be written

$$y = .05x$$

or, more generally

$$y = bx \ldots\ldots\ldots\ldots (2)$$

The *power regression* or "allometry equation" may be expressed

$$y = cx^k \ldots\ldots\ldots\ldots (3)$$

where y and x represent the two variables as in (1); k (a constant) is the constant percentage that each y-increment is of the preceding increment; and c (a constant) is the slope of the tangent to the curve when $x = 1$. (The magnitude of c depends on the units of measurement; it is an arbitrary constant.) Note that the curve will always pass through the origin, since if $x = 0$ the right side of (3) becomes zero and $y = 0$. Lines corresponding to (3) will always form a straight line on logarithmic coordinates and, except in special cases, a curve on arithmetic coordinates.

Obviously, (2) is a special case of (3) where $k = 1$.

Transformation of (3) to logarithms yields

$$\log y = \log c + k \log x \ldots (4)$$

which is of the same form as (1), with $\log c = a$ and $k = b$.

An example of a power regression is given in Fig. 2. In the example, $c = 0.2$ and $k = 0.9$. This curve is convex; y is growing at a

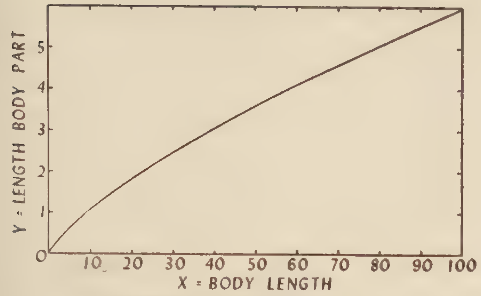

Fig. 2. Hypothetical example of a power regression of the type $y = cx^k$.

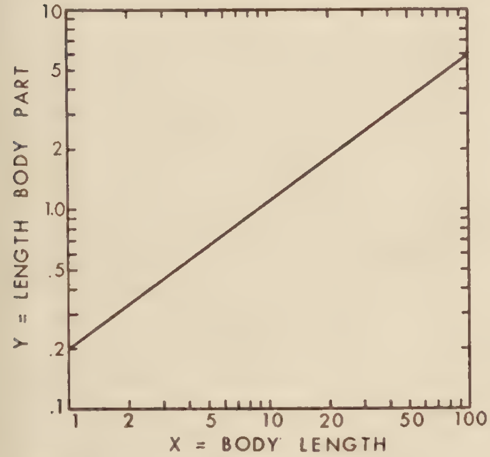

Fig. 3. Hypothetical example of a power regression of the type $y = cx^k$.

slower relative rate than is x. If $k > 1.0$, the curve is concave; y is growing at a faster relative rate than is x. If $k = 1$, the curve is a straight line.

The same curve is plotted on logarithmic coordinates in Fig. 3. (It is usually easier to plot directly on log paper, rather than to look up the logarithms and plot their values on arithmetic coordinates.) In this transformation, k = the slope of the line. A slope of 1.0 (i.e., at 45° to the x-axis) indicates a curve whose equation is represented by (2). When $k > 1.0$ the angle of the curve to the x-axis will exceed 45°.[3]

The general expression which may be written to include (1) and (3) is

$$y = a + cx^k \ldots\ldots\ldots (5)$$

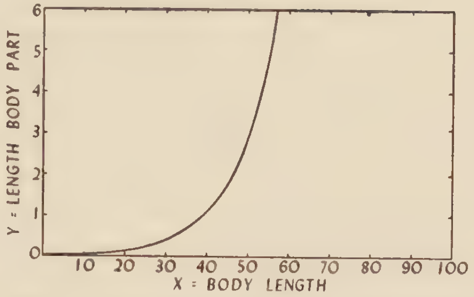

Fig. 4. Hypothetical example of an exponential regression of the type $y = pe^{kx}$.

In the case of (1) $k = 1$ and in the case of (3) $a = 0$.

The *exponential regression* may be represented by

$$y = pe^{kx} \ldots\ldots\ldots\ldots (6)$$

where y and x represent the two variables as in (1) and (3); p (a constant) $= y$ when $x = 0$; e is the base of natural or Napierian logarithms; and k (a constant) is the percentage change in y per unit change in x. Lines corresponding to (6) will always give a straight line on semi-logarithmic coordinates and a curve on arithmetic coordinates. Equations of type (6) may be recognized as the "compound interest law."

Transformation of (6) to logarithms yields

$$\log y = \log p + k(\log e)x \ldots (7)$$

which is, again, of the same form as (1), with $\log p = a$ and $k \log e = b$.

An example of a curve of the type (6) is shown in Fig. 4 on arithmetic coordinates and in Fig. 5 on semi-logarithmic coordinates. In the example $p = 0.02$ and $k = 0.1$. Note that the log scale is on the y-axis.

Relationships of this form are relatively uncommon and obviously could not obtain over a large range of x-values, since the body part would eventually become exceedingly larger than the body.

The exponential relationship is more commonly encountered in the form

$$x = pe^{ky} \ldots\ldots\ldots\ldots (8)$$

But since one is interested in estimating y from x, this may be re-written as

$$y = \frac{-\log p}{k(\log e)} + \frac{1}{k(\log e)} \times \log x \ldots (9)$$

---

[3] As Morrow (1952) and others have pointed out, when the dependent variable involves two dimensions (such as breadth and depth) a 45° curve on logarithmic coordinates will result when $k = 2$. Similarly, when the dependent variable involves three dimensions, a 45° curve will result when $k = 3$.

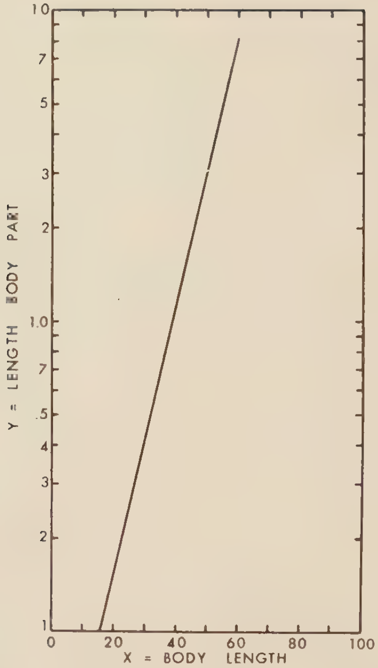

Fig. 5. Hypothetical example of an exponential regression of the type $y = pe^{kx}$.

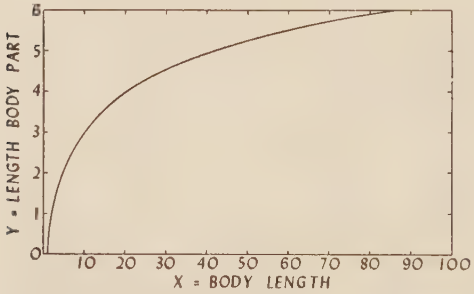

Fig. 6. Hypothetical example of an exponential regression of the type $x = pe^{ky}$.

Here the log scale is on the x-axis.

Again, this is the form of (1), with $\frac{-\log p}{k(\log e)} = a$ and $\frac{1}{k(\log e)} = b$. Also, since $e^0 = 1$, when $y = 0$, $x = p$. The curve cannot go through the origin unless $p = 0$ and in that case (8) would reduce simply to

$$x = 0$$

The curve (8) is, in fact, asymptotic to the y-axis.

An example of a curve of form (8) is given on arithmetic coordinates in Fig. 6 and on semi-log coordinates in Fig. 7. In the example $p = 1.0$ and $k = 0.75$.

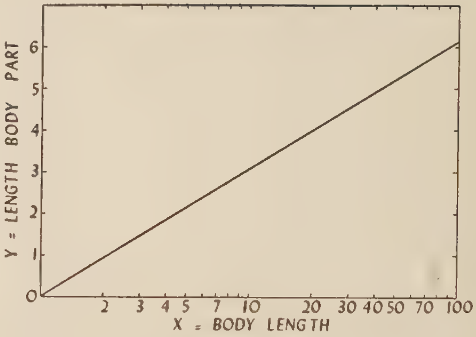

Fig. 7. Hypothetical example of an exponential regression of the type $x = pe^{ky}$.

Judging from published data, the relationship of size of the body part to body size in fishes will generally approximate very closely equations of either type (1), (3) or (8). (Although this discussion has been restricted to fishes, it is well known that the methods discussed are widely applicable to both vertebrates and invertebrates.) Further discussions which are pertinent to this, or closely allied problems, have been given by Barnes (1952), Brody (1945), Child (1941), Huxley (1932), LeGros Clark and Medawar (1945), Martin (1949), Simpson and Roe (1939), Thompson (1943) and Winsor (1946).

While there has been rather wide use of the "allometry equation," (3), especially in relative growth studies, its use has been largely empirical. So far as I have been able to discover, there has been no satisfactory theoretical explanation of why the relative growth of body parts should follow any of the regression equations given above, or any other for that matter (but see von Bertalanffy, 1949). The significance of these observed relationships is not germane to discussion of appropriate methods of representing empirical data. However, I believe a promising approach to this fundamental problem of relative growth could be made under the reasonable assumption that the juveniles, for example, and the adults of any particular species are well suited for existence in their respective environments. Considering these two known forms (juvenile and adult), with differing body proportions, as fixed "beginning" and "end points", the various ways by which the necessary changes in body form could be accomplished could then be investigated.

While perhaps not strictly pertinent to this discussion, any description and interpretation of relative growth data should take into account the following: (1) The data may be representative of phenotypes rather than genotypes (Martin, 1949; Tåning, 1952). (2) Length, which is commonly used as a measure of size, represents only one dimension and may, therefore, not be the best measure of size. (3) Various life history stages may involve different growth stanzas.

RATIOS VS. ORIGINAL MEASUREMENTS

Examples of dubious conclusions or, at the very least, incomplete utilization of data, arising from the use of ratios rather than original measurements are to be found throughout the literature. Before proceeding to some of these, I should like to provide a hypothetical example. For the sake of simplicity I shall restrict the example to data forming a rectilinear regression of type (1).

The example previously used, shown as line 1 in Fig. 1, has a slope of 0.05 and passes through the origin. Also shown in Fig. 1 are two additional lines having the same slope as line 1, but with one having a y-intercept of $+2$ (line 2) and the other having a y-intercept of -2 (line 3). The lines of this family differ only in intercept; they all represent the same change in y per unit change in x. (In actual practice, one is often considering only a sample drawn from a range of adult sizes. In such a case the y-intercept and the slope of the line, b, are parameters of the regression for *only* that size range sampled. The use of the y-intercept as a parameter should not be taken to imply that the regression is extrapolated back to estimate the size of the body part when body size was zero.)

The three main features of these lines (rectilinearity, intercept differences and identity of slopes) are apparent when they are plotted in this form. Furthermore, there are conventional methods of characterizing such lines, for defining variance and for comparing lines (see Snedecor, 1946 and Kendall, 1948, for example). This is not true when ratios are used.

The three lines of Fig. 1, are shown again in Fig. 8, but in the latter figure, the ratio "length of body part/body length" is plotted as the dependent variable and body length is plotted as the independent variable. In line 1, y increases at the rate of 0.05 x and this is reflected in the horizontal line at 0.05. Lines 2 and 3 also increase at the rate of 0.05 x, but do not form a horizontal line in the ratio plot. They have large positive (line 2) or negative (line 3) values for small values of x and decrease in absolute magnitude as x increases. They are in fact, asymptotic to the horizontal line at 0.05. The deviation, in the ratio plot, of lines 2 and 3 from line 1 arises from the fact that they do not pass through the origin. Their intercepts are, percentagewise, large when x is small and small when x is large. For some purposes, identification of specimens for example, it would be pertinent to observe that in the species represented by line 2 the length of body part relative to body length does decrease with increasing body length. But this is solely the effect of the positive y-intercept and it would be inaccurate to conclude that the rate of change in size of body part relative to body length was decreasing. In the literature this "intercept effect" in ratio plots is often erroneously interpreted as indicating allometric growth.

The ratio plot does not yield any information which cannot be obtained from the plot of original variates, the curvilinearity (when there is an intercept differing from zero) makes difficult, if not impossible, the computation of variance and comparison of lines and, finally, a likely source of error in interpretation is introduced.

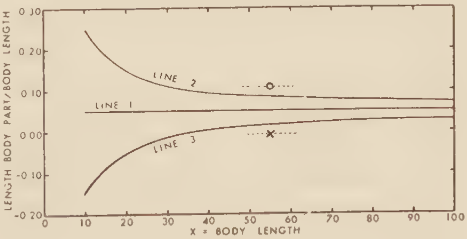

Fig. 8. Hypothetical examples of rectilinear regressions of the type $y = a + bx$, with the ratio y/x plotted as the dependent variable.

SOME EXAMPLES

In systematic works, when only one or a few specimens are available, it is customary to present tables of data in which, for each specimen, the actual standard length is given, but all other measurements are expressed in per cent or per mille of standard length. Examples of such tables may be found in a paper by Schultz (1949). When small numbers of specimens are involved it is possible to present complete data (even if these are customarily given in the form of ratios), but it is impossible to make use of regression analysis simply from lack of data. However, even when large series of specimens are available it often happens that only a few are measured (see Table 22 in Schultz (1944), for example).

When large series of specimens are used it is generally impossible to present all data owing to space limitations, and some form of condensation is required. Even though the data may be represented concisely by regression equations and standard errors, one commonly finds tables in which the mean and ranges of the ratios are given. An example of such tables is Table III of Hubbs and Bailey (1940), which pertains to six forms of *Micropterus*. They give the means and ranges of ratios, but do not indicate the actual size of the fishes to which the ratios pertain (except for the mean and range for one subspecies). Many of these ratios are changing with increase in fish length, as they indicate, and the table is accordingly difficult to interpret.

The pitfalls of using arithmetic averages of ratios have frequently been described in numerous statistical texts. The average ratios for lines 2 and 3 in Fig. 8 are indicated by the short broken lines. Obviously, the average for line 2, for example, is below the true values at small fish sizes and above the true values at large fish sizes. The average ratio for average fish size exceeds the true value for line 2 (circle) and for line 3 (x). These anomalies are, of course, in this case the result of intercepts differing from zero. (However, when the size range in individual samples is small and when the small size range is essentially the same for all samples to be compared, the use of ratios will probably lead to the same conclusions as would the use of regression analysis.)

Parr (1949) has proposed a rather complicated system for representing body proportions of fishes with reference to growth changes. Without wishing to comment on the utility of his proposed system, I should like to point out that unnecessary complications have been introduced by the use of ratios. For example, in his Fig. 2c there are plotted the ratios of head length/standard length against standard length of *Alepocephalus girardi*. To these points he has fitted two straight lines with a break at about 600 mm. standard length. It seems likely that these points may be better fitted by a smooth curve similar to line 3 in my Fig. 8. In fact, if Parr's data are replotted as original variates, it is evident that the curvilinearity of the ratio plot is caused by the positive intercept, just as in line 3, Fig. 8. It may also be mentioned that the point which Parr considered to be anomalous in his plot is not anomalous in a curvilinear ratio plot nor in the rectilinear regression of original variates.

A series of papers on yellowfin tunas by Schaefer (1948, 1952) and Schaefer and Walford (1950) might equally well be considered as systematic or as racial studies. In addition to including all original data, these studies have made use of regression analysis of original measurements. Reference to these works will clearly demonstrate the objective advantages of the methods used. As a result of these studies, these authors concluded that the samples from off Angola, off Central America in the Pacific, and from the vicinity of the Hawaiian Islands represent distinct populations. The taxonomic question of the rank of these distinct populations was deferred pending further studies.

That the advantages of the methods of regression analysis are not universally appreciated is evidenced by Ginsburg's (1953) treatment of the yellowfin tunas. He elects not to use regression analysis and puts the data of Schaefer (1952) and Schaefer and Walford (1950) ". . . . in a form comparable to that usually employed in taxonomic treatises. . . ." (Ginsburg, 1953: 4); i.e., in the form of frequency distributions of ratios by selected length intervals. This, of course, is a kind of primitive regression analysis with none of the quantitative advantages of the methods used by Schaefer and Walford. It does, however, represent an advance over the use of averages of ratios in that size-specific changes are recognized.

Mayr, Linsley and Usinger (1953: 137–8) stated that ". . . . ratios are more useful as taxonomic characters than direct measurements, because the variable factor of size is minimized. . . ." And, further, that "Care should be taken to check the rate of increase of each of the measurements used in a ratio, because different parts of the body of an animal commonly grow allometrically." In an example they give the ". . . . allometry is so slight that it does not affect the validity of the conclusions for taxonomic purposes. In some cases, however, allometry renders a particular pair of characters completely useless for taxonomic purposes." While they correctly point out that allometric growth vitiates the use of ratios in regression analysis, the use of original variates with appropriate transformation in regression analysis will not preclude the use of data involving allometric growth.

Racial studies generally involve larger series of specimens than does taxonomic research at higher systematic levels, and the opportunities to make use of regression analysis are consequently greater. Examples of the use of regressions of original variates may be found, in addition to some of the papers cited above, in the works of Godsil and Greenhood (1951) on Pacific yellowfin tuna, Kesteven (1942) on the Australian mullet, Roedel (1952) on Pacific mackerel and Wilder (1952) on brook trout.

Rounsefell (1930) has compared the head lengths of Pacific herring from different localities, by considering the regressions of head length/body length ratios on body length. These regressions are curvilinear and he interpreted the fact that the curves did not overlap as indicative of differences, since . . . . "the differences between the curves cannot be calculated mathematically owing to the differences in slope. . . ." (Rounsefell, 1930: 270). If the original variates are plotted, rectilinear regressions result which can be compared by the conventional methods. The curvilinearity of the ratio plots results, again, from the fact that the regressions of original variates have *y*-intercepts differing from zero.

As stated above, students of relative growth seem, in general, to have been aware of the limitations of ratios and to make use of the statistical tools available. Examples of such studies are those of Martin (1949) on various species, Morrow (1952) on striped marlin, and Shapiro (1943) on various scombroid fishes.

Morrow (1951), in studying the relative growth of the longhorn sculpin, has considered the regression of the body part/standard length ratio on standard length. With regard to the eye he stated (1951: 20): that it ". . . . shows a pronounced degree of negative allometry in the small specimens and slight negative allometry in the larger animals. This is of particular interest, for there is an abrupt change in the slope of the line of trend at about 80 mm. S.L., indicating that a marked change in the manner of growth of this organ occurs early in the second year. . . . Apparently the eye grows rapidly during larval and post-larval development and then slows abruptly, resuming growth at nearly the same rate as the rest of the body during the second year."

Actually, his ratio plot is fitted better by a continuous curve rather than by two straight lines. The regression of original variates proves to be rectilinear with a positive *y*-intercept. The latter, of course, accounts for the curvilinearity of the ratio plot. Therefore, the rate of growth of the eye in relation to the rate of growth of the body does not change over the size range studied. Dr. Morrow has kindly re-examined these data and has informed me (personal letter dated September 29, 1953) that he is in complete agreement with my interpretation.

SUMMARY

The relation of size of body part to size of body in fishes will generally conform to either rectilinear, power or exponential equations. The latter two may be easily transformed to straight lines by the appropriate use of logarithms. For such straight-line regressions there are conventional methods of characterizing the lines, computing their variance, and comparing them.

Systematic studies and, to a lesser extent, racial and relative-growth studies often present data on body proportions in the form of ratios, averages of ratios, or regressions of ratios. These methods, as opposed to the regression analysis of original variates, are inefficient and may often lead to erroneous interpretation. A simple hypothetical example, as well as several examples from the literature, demonstrates the point.

Acknowledgments

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NOTES ON THE PRECISION OF A MODIFIED ROUTINE NITRATE-NITRITE ANALYSIS

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ABSTRACT

Factors responsible for difficulties in using the strychnidine method for an analysis of nitrate-nitrite content of sea water have been investigated. It has been demonstrated that their effects can be minimized and that the ease of analysis is materially increased by certain modifications, one of which is the adjustment of the concentration of nitrate by dilution to bring the optical density within the best working range of the photometer used. The largest single source of error was found to be variation in the rate of heat formation during the mixing of the sample and reagent, which could be minimized by following the mixing procedure recommended. It is believed that this work offers improved precision without affecting the value of the technique as a rapid routine method for large-scale investigations.

In using the strychnidine method for analysis of nitrate-nitrite in sea water, we experienced many of the same difficulties encountered by other operators. In an effort to minimize these difficulties, a modified method has been developed which is now employed in the laboratory of the Gulf Fishery Investigations. Actually, it is a modified version of the analysis prescribed by Zwicker and Robinson.[1]

This modification controls color densities of the reagent-sample mixture so that the range of concentrations found in sea water can be determined by using 3 ml micro cells (cylindrical cell 6.75 cm long and 1.19 cm inside diameter) in a Fisher A. C. Electrophotometer. The mixture is obtained by diluting the water sample with two parts of distilled water and then adding this diluted sample to an equal volume of a reagent consisting of 0.3 millimole of strychnidine per liter of concentrated sulfuric acid.

[1] Zwicker, B. M. G. and R. J. Robinson. 1944. The photometric determination of nitrate in sea water with a strychnidine reagent. J. Mar. Res., *5:* 214–231. They used the Zeiss-Pulfrich photometer equipped with 0.1–15 mm variable depth cell. Their procedure was as follows:

Equal volumes of reagent and sample were carefully mixed in aged pyrex tubes by four careful but rapid transfers from one to the other. The hot mixtures were immediately placed in the dark for three to five hours. Measurements were then made with a photometer.

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This reagent is suitable for determining concentrations found in waters which range from 0 to about 45 microgram atoms of NO_3-NO_2 nitrogen/liter (μg-at NO_3-NO_2-N/l). The -log T readings for this range cover practically the entire scale of the electrophotometer and at the same time permit the use of a calibration curve having the best possible slope. Thus, maximum efficiency of the photometer is achieved. At concentrations above 45 μg-at/l, the slope flattens too much for use.

The dilution of samples does not necessarily mean that all errors will be increased proportionally. Actually, the dilution moves the concentration of many samples to a more sensitive region of the NO_3-NO_2 calibration curve.

Zwicker and Robinson recommended that the strength of the reagent and the depth of the cell be dependent upon the range of NO_3-NO_2 concentration in the sample in order to utilize the optimum operating conditions of reagent and photometer.[2] In our routine sampling of hundreds of water samples having the range of NO_3-NO_2 concentration found in the Gulf, their recommendation would be impractical since it would necessitate a preliminary investigation of all samples to approximate the magnitude of the NO_3-NO_2 concentration.

A chemist and his helper can easily run 200 determinations in an eight-hour period when employing our modification, which is as follows:

1. With a 1 ml pipette, transfer 1 ml of sample which has had no preliminary preparation, such as filtration, etc., into each of two 10 ml pyrex test tubes (for duplicates).
2. With a 3 ml automatic pipette, add 2 ml of distilled water to each of the 10 ml tubes.
3. Using a 5 ml automatic pipette, add 3 ml of strychnidine reagent to each tube. To prevent boiling during this addition, tilt the tube to about a 45° angle and allow the reagent to run down the inside so that it forms a layer under the water sample. It is important that this step be performed with great care to avoid unnecessary mixing of reagent and sample.
4. With the aid of a 15 ml pyrex tube, mix by gently pouring the contents of each tube into the mixing tube and back again only once. It is suggested that about 15 mixing tubes be used in rotation and that each tube be allowed to drain after use.

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[2] Their recommended procedure for the Zeiss-Pulfrich photometer follows:

NO_3 *range* (μg-at/l)	*Strychnidine* (millimoles/l)	*Sample* (ml)	*Size of Test Tube* (mm)	*Standing Time* (hours)	*Thickness of Cell* (stratum, mm)
0.2–4	0.10	14	20 ×155	4–24	50
2.5–10	0.10	3	13 ×100	2–28	10
5–15	0.50	3	13 ×100	2–5	5
1.2–40	1.0	3	13 ×100	2–5	2
2.5–75	5.0	3	13 ×100	2–4	1

5. Store samples in darkness for four hours.
6. Check color density with the Fisher A. C. Electrophotometer by using 3 ml micro cells and 525 mμ "B" filter.
7. Check the results against standard controls which are run with the samples and which are interspersed among them during the reading of color densities.

ESTIMATE OF PRECISION OF THE METHOD

An estimate of precision was obtained by running a series of checks within the range of values that are possible with a Fisher A. C. Electrophotometer equipped with a 3 ml micro cell and with a reagent containing 0.3 millimole of strychnidine in a liter of concentrated sulfuric acid. This range includes concentrations from 0 to 15 μg-at/l of nitrate.

The range was covered in 1 μg-at/l steps. Approximately 50 replicate determinations were made on each of the 16 concentrations that were checked. Color density differences between samples and distilled water were read directly from the electrophotometer in -log T units after which they were converted to μg-at/l units by assuming a constant slope between two adjacent sets of standards. An estimate of precision for the concentrations tested is tabulated in column 4 of Table I.

TABLE I. Statistics Pertaining to NO_3-NO_2 Analyses at Various Concentration Levels

Concentration level	N	$\bar{X}$	S	l_1	l_2
0	55	0.000	0.1551	−0.0558	0.0558
1	52	1.004	0.1171	0.9606	1.0474
2	55	1.987	0.1156	1.9454	2.0286
3	52	2.988	0.1131	2.9461	3.0299
4	51	4.022	0.1640	3.9605	4.0835
5	56	4.993	0.2463	4.9052	5.0808
6	53	6.030	0.0799	6.0007	6.0593
7	55	6.980	0.2791	6.8796	7.0804
8	56	8.014	0.1939	7.9449	8.0831
9	53	9.002	0.3054	8.8899	9.1141
10	51	9.998	0.3465	9.8682	10.1278
11	43	11.040	0.2927	10.9197	11.1603
12	54	12.030	0.3937	11.8869	12.1731
13	53	13.028	0.3478	12.9003	13.1557
14	46	13.974	0.3022	13.8540	14.0940
15	57	14.974	0.3807	14.8396	15.1084

N—Number of replicates.
$\bar{X}$—Average of replicates in μg-at NO_3-NO_2-N/l.
S—Standard deviation.
l_1; l_2—Fiducial limits of $\bar{X}$ at a probability level of .01.

In the modified routine analysis, the precision would be approximately one-third that shown in column 4 of Table I because all samples are diluted with two parts of water; hence, the standard deviation of the sets would be increased by three. Also, the difference in error of the two methods due to volumetric difference would have to be included. This, as shown in Table II, is negligible. Based on these facts, Table III has been constructed to show the precision that can be expected from routine analysis.

TABLE II. PRECISION OF VOLUMETRIC MEASUREMENTS

No. 1 *Steps involved in routine analysis.*

1.—1 ml sample delivery using 1 ml pipette.
2.—2 ml H_2O delivery using 3 ml automatic pipette.
3.—3 ml reagent delivery using 5 ml automatic pipette.

Step	1	2	3
N	31	33	30
S^2	2.35×10^{-5}	6.36×10^{-5}	1.69×10^{-4}

$$S^2 \text{ due to volumetric deviation} = \frac{2.35 \times 10^{-5}}{6} + \frac{6.36 \times 10^{-5}}{3} + \frac{1.69 \times 10^{-4}}{2} = 1.096 \times 10^{-4}.$$

S due to volumetric deviation $= .0105$.

No. 2 *Steps involved in estimating precision.*

1.—3 ml sample delivery using 5 ml automatic pipette.
2.—3 ml reagent delivery using 5 ml automatic pipette.

Step	1	2
N	20	30
S^2	6.42×10^{-5}	1.69×10^{-4}

$$S^2 \text{ due to volumetric deviation} = \frac{6.42 \times 10^{-5}}{2} + \frac{1.69 \times 10^{-4}}{2} = 1.166 \times 10^{-4}.$$

S due to volumetric deviation $= .0108$.

N—Number of replicates. S^2—Variance. S—Standard deviations..

ESTIMATE OF PRECISION OF EACH STEP IN THE NITRATE DETERMINATION

The precision of the modified technique was estimated by determining the accuracy that could be expected from each individual step. Experiments were conducted in which the various steps of the technique were deliberately varied to considerable extents. The effects of these alterations on the final nitrate concentration were then ascertained.

Human and instrumental errors introduced in reading color density differences were estimated by measuring the deviation that occurred in reading sets of replicates from a series of standards. A standard was made up and a portion poured off and checked in the photometer.

TABLE III. STATISTICS PERTAINING TO ROUTINE NO_3-NO_2 ANALYSIS

Concentration Level	N	S^2	$\bar{X}$	S_1^2	S_2^2	$S^2-(S_1^2+S_2^2)$	l_1	l_2
0	55	0.2406	0.000	0.0036	0.0001	0.2369	−0.0558	0.0558
3	52	0.1234	3.012	0.0036	0.0001	0.1197	2.8818	3.1422
6	55	0.1202	5.964	0.0036	0.0001	0.1165	5.8362	6.0858
9	52	0.1153	8.964	0.0049	0.0001	0.1103	8.8383	9.0897
12	51	0.2423	12.066	0.0049	0.0001	0.2373	11.8815	12.2505
15	56	0.5461	14.979	0.0081	0.0001	0.5379	14.7156	15.2424
18	53	0.0574	18.090	0.0121	0.0001	0.0452	18.0021	18.1779
21	55	0.7013	20.940	0.0289	0.0001	0.6723	20.6388	21.2412
24	56	0.3385	24.042	0.1521	0.0001	0.1863	23.8347	24.2493
27	53	0.8394	27.006	0.0625	0.0001	0.7768	26.6697	27.3423
30	51	1.0854	29.994	0.1156	0.0001	0.9697	29.6046	30.3834
33	43	0.7720	33.120	0.1849	0.0001	0.5870	32.7591	33.4809
36	54	1.3912	36.090	0.2704	0.0001	1.1207	35.6607	36.5193
39	53	1.0952	39.084	0.3600	0.0001	0.7351	38.7009	39.4671
42	46	0.8217	41.922	0.2304	0.0001	0.5912	41.5620	42.2820
45	57	1.3003	44.922	0.3025	0.0001	0.9977	44.5188	45.3252

Concentration Level—Approximate Concentration in μg-at NO_3-N/l Tested.

N—Number of replicates.

$\bar{X}$ —Average of replicates expressed in μg-at NO_3-N/l.

S^2—Variance.

S_1^2—Variance due to instrumental and operational deviation.

S_2^2—Variance due to volumetric deviation assuming all deviations are accumulative.

l_1; l_2—Fiducial limits of $\bar{X}$ at a probability level of .01.

The sample was then removed from the instrument and poured back into the original batch of standard. This cycle was repeated approximately 50 times for each concentration. Instrumental and operational errors were based on deviation in these sets of readings. The standards used for this check consisted of various dilutions of a nonfading red compound (red ink). This eliminated possible deviation due to color fading during the time required to read a set of replicates. The results, tabulated in column 5 of Table III are also presented in Fig. 1.

The errors involved in pipette deliveries result from variations in measuring: 1 ml of sample with a 1 ml pipette, 2 ml of distilled water with a 3 ml automatic pipette, and 3 ml of reagent with a 5 ml automatic pipette. The variation that can be expected with these three instruments was estimated by measuring equivalent amounts of distilled water for the 1 and 2 ml measurement and of sulfuric acid for the 3 ml reagent measurement, after which the accuracy of each measurement was determined by weight on an analytical balance having a sensitivity of approximately 1/10 mg.

The results of this check are given in Table II and in column 6 of Table III. The effect of deviations in sample and reagent measurements on the final nitrate concentration was determined by running several series of checks in which variations were deliberately intro-

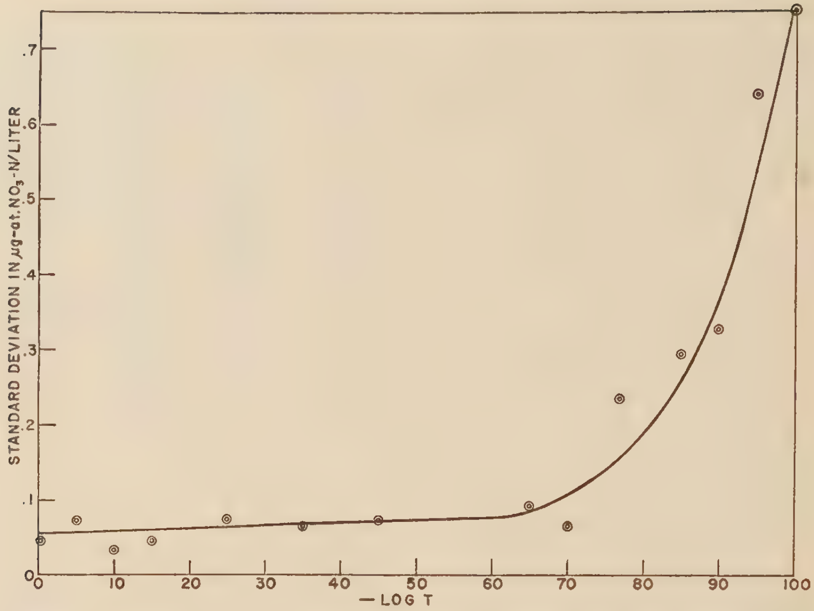

Figure 1. Deviation in NO_3 concentration caused by instrumental and operational errors.

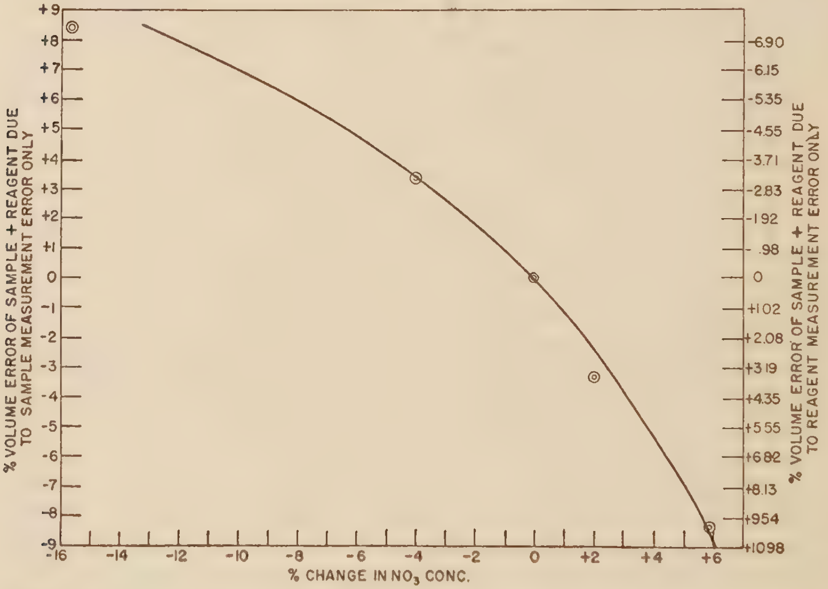

Figure 2. Per cent errors in NO_3 concentration caused by volumetric deviations.

duced. The results, which show variation in nitrate concentration vs. variations in sample and reagent measurements, are presented in Fig. 2.

We found that variation in the rate of heat formation during the mixing of the sample and reagent is the greatest single factor that affects the precision of the results. Investigation has shown that the degree of variation in color formation of replicate samples is dependent on the rate of removal of the heat produced during the mixing operation. A high rate of increase in temperature results in a minimum color density, whereas a low rate of increase results in a maximum color density. By standardizing the mixing operation, it has been possible to reduce greatly the variability due to heat, thereby increasing the precision of the method.

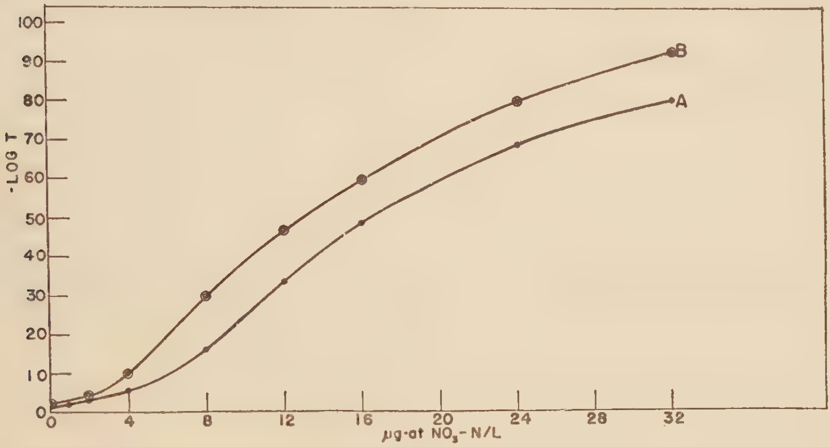

Figure 3. NO$_3$ calibration curve showing effect of rate of heat formation on color development. *A*—high rate of heat formation. *B*—low rate of heat formation.

The effects of high and low rates of heat formation are demonstrated in two calibration curves, *A* and *B* of Fig. 3. Both curves were made from a single set of standard samples and from the same batch of reagent. The determination of values for the two curves was based on the average of 10 replicates run alternately to minimize errors due to time difference. A maximum rate of heating was obtained by mixing the samples and reagent rapidly (see Curve *A*). A minimum rate was obtained by carefully adding reagent to sample in such a way that two distinct layers were formed. These were then mixed by pouring them into a "mixing" tube and back into the original tube; thus, the mixture was poured only twice, from original tube to mixing tube and back again.

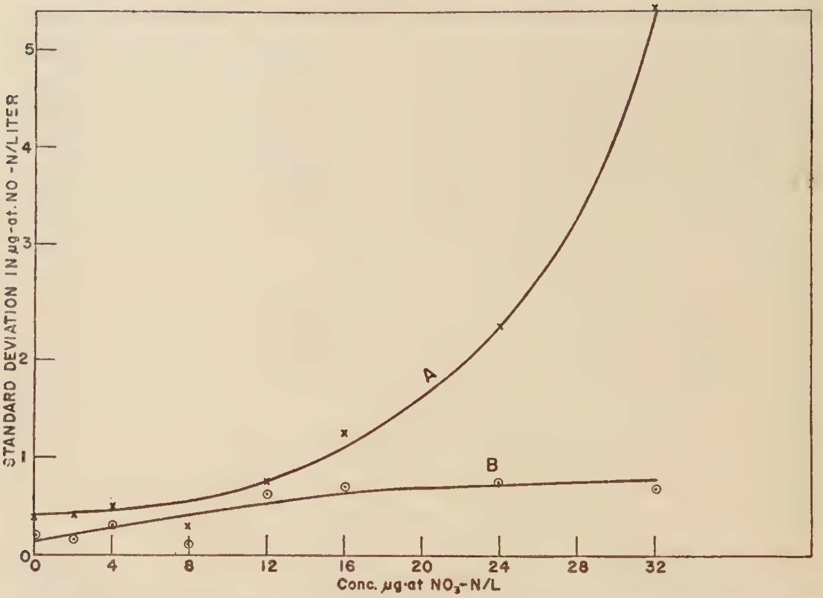

Figure 4. Comparison of standard deviations at various NO_3 concentration levels: *A*, when rate of heat formation during the mixing of reagent and sample is high; *B*, when the rate of heat formation is low.

The range of values represented by the horizontal distance between curves *A* and *B* represents the deviation that could occur within a set of replicate samples if an operator were unfamiliar with the relationship that exists between rate of heat formation and color formation. A comparison of the standard deviation of the two sets is shown in Fig. 4.

The low degrees of variation exhibited by *B*, as compared to *A*, indicate that careful mixing is necessary if good precision is to be maintained.

DISCUSSION

The entire check on precision of the method could not be completed during one session. Had it been possible, then the average of the 16 sets could have been used in the construction of a calibration curve, thus eliminating the necessity of arriving at slope values by assuming straight line relationships between two sets of values. The fact that all 16 points do not form a smooth curve emphasizes the importance of including a set of standards with every run of samples. We found that there was considerable day-to-day variation in the density of color formation, probably due to temperature difference, methods of mixing sample and reagent, and other conditions that would be difficult to control.

A four-hour color development time was allowed for all determinations. This time was based on a check of color density vs. time for concentrations of 0, 6, 18, 25, 30, and 45 μg-at NO_3-N/l. Results show that rate of development at 30° C became minimal between the fourth and fifth hour. The room temperature during the experiments was approximately 30° ± 2° C.

The final nitrate concentration varies almost directly with the deviations normally expected in the measurement of sample, reagent, and distilled water. This is illustrated in Fig. 2, in which volumetric errors have been deliberately introduced. This direct relationship was assumed to be the case.

A large percentage of the total deviation incurred in the modified technique cannot be accounted for by instrumental, operational, or volumetric errors. The data in columns 3 and 7 of Table III demonstrate that variation in rate of heat formation during the mixing of sample and reagent probably accounts for a large percentage of this difference even though efforts were made to minimize this effect.

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Some Considerations Regarding the Nutrition of Marine Fish Larvae.

By

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I. Introduction.

It was reasoned by Hjort (1914) that the size of a year-class of marine fishes is determined during the very early developmental stages. Although subsequent studies have tended to support Hjort's contention, the actual causes of success or failure of a year-class have not been determined.

One of the most important factors for survival is food. There have been only a few detailed studies of the food habits of marine fish larvae. Lebour (1916—18, 1919—22 b, and 1919—22 c) examined the gut contents of many fish larvae representing a large number of marine species. Lebour (1919—22 c: 262) stated:— "One finds that certain copepods and other Entomostraca constitute by far the larger part of the food of nearly all the very young fish, and that usually each species of fish selects its own favourite food to which it keeps, indiscriminate feeding seldom or never taking place, and one can usually assign to each fish its own particular food. The diet of the fish, however, depends to some extent on the size of the mouth and gullet and in a few fish a unicellular diet is the rule up to a considerable size.

Few fish are vegetarians, and it is unusual for any but the youngest fish to eat diatoms . . . Very young herring and sprat and a few others often contain green remains which probably belong to some algae, and occasionally diatoms can be recognized in this, but even before the yolk sac is absorbed the gut may contain larval molluscs and small crustaceans, as in the young herring."

Lebour's findings have lent much weight to the current view that early larvae of marine fishes depend almost exclusively upon food particles of relatively large size.

Fish larvae kept in laboratory tanks display characteristic patterns

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of feeding behaviour. Lebour (1919—22 a) described such patterns for several species. Other investigators engaged in the rearing of larval fishes have also noted that among the very young, feeding is apparently a deliberate process. I have kept larvae of a number of species in laboratory containers and their behaviour certainly suggested that they were dependent upon food particles 40 to 50 μ in diameter, or larger.

II. Food Habit Studies.

Studies of the food habits of fish larvae have been conducted by both observational and experimental methods, (cf. Lebour, 1919—22 a and 1919—22 b). There are some serious limitations in each of these methods.

Crude observations of the gut contents of larvae collected from nature show what microscopic forms have been recently ingested. They do not show, however, the extent to which the ingested particles nourish the larvae. In the larval guts many organisms can be found which show no erosion of the integument or other indication that they were being digested at the time of collection. To conclude that easily identifiable objects in the gut represent *the* food of that particular larva always calls for a measure of faith.

It is extremely difficult to establish an approximation to a natural pelagic habitat that will be satisfactory for controlled experiments. There is always a question as to what distortion of behaviour may be induced by the unnatural environment. With few exceptions, it has in the past been impossible to rear the larvae of marine fishes through the period during which they first begin to feed, and comparative studies bearing upon that period have not yet been made.

Both observational and experimental methods, but particularly the experimental, are limited by the fact that the choice of food will necessarily be confined to that which is available to the larvae.

III. Pütter's Theory.

Among the concepts of nutrition of aquatic animals there has perhaps been none so controversial as that known as "Pütter's Theory". Pütter investigated experimentally the nutrition of a number of aquatic animals from several systematic groups and came to the conclusion that their survival depended heavily upon direct utilization of the dissolved organic constituents of the water. Pütter concisely expressed his beliefs at the conclusion of his monograph (1909 a: 147):— "Die Ernährung eines grossen Teiles der Formen aller Stämme vollzieht sich nicht in der Weise, wie man es bisher, in grosser Analogie mit den Säugetieren und Vögeln annahm; d. h. dass geformte Nahrung aufgenommen, durch die Verdauung gelöst und gespalten und in diesem Zustande resorbiert wird, sondern eine grosse Anzahl von Tieren, speziell die absolut kleinen Formen aller Stämme nehmen, soweit sie im Wasser leben, ihre Nahrung direkt in gelöster Form aus dem Wasser auf."

Pütter published a number of other papers in support of his theory (cf. references in Krogh (1931) or Bond (1933)).

Contemporaneously with, and subsequent to, Pütter's research, a number of investigators contributed to this subject. The findings of these other investigators were largely negative. When the matter was reviewed by Krogh (1931) it was concluded that animal forms higher than protozoa and sponges were without mechanisms for directly utilizing dissolved organic nutrients, at least under any approximation to natural conditions, where such solutes are present in only very dilute concentrations.

IV. Some Factors to be Considered.

Pütter's and subsequent research on fishes.

Pütter (1909 a and 1909 b) described his investigations of the nutrition of five forms of marine fishes, *Hippocampus*, *Balistes*, *Scorpaena*, *Gobius*, and *Heliastes*. Since that time many animals have been used as subjects for testing Pütter's Theory and some of the tests have been conducted with extreme refinement (cf. Bond, 1933). Is is over 40 years, however, since *marine* fishes were subjected to tests of this theory (Moore *et al.*, 1912).

Moore *et al.* experimented with several marine animals to determine whether or not they could utilize dissolved organic matter present in the water. Only one of their animals was a fish, *Blennius*. Their work was carefully executed but limited in scope (a single specimen weighing about 10 g. in 2800 ml. of Chamberland filtered sea water for a period of 24 hours), and although it did demonstrate that the fish did not gain from dissolved organic matter, there remains the possibility that it might have done so under somewhat different circumstances.

Incidence of particulate feeding.

Summarizing his section devoted to supply and demand of food among aquatic animals, Krogh (1931: 419) stated:— "... both among the fishes and among the invertebrates we have to do with carnivorous animals which take food only occasionally, and the intestine of which is therefore empty when digestion of a prey is finished. In many fishes the intestine is empty in the morning, because food is taken only during the day ... For a number of the fish which, according to Pütter, would take only quantitatively insignificant amounts of particulate food, it can now be stated on the authority of Blegvad and Marie Lebour, that they can and do obtain a sufficiency of such food, but the fact remains that in a number of cases the information with regard to the quantities of food which are eaten is very incomplete."

Lebour (1919—22 c: 269) stated:— "The large number of empty guts in some of the young fish, especially the clupeoids, is striking. Green food remains are often found in the very young sprat, but the herring and pilchard are more often empty." and (1919—22 d: 458):— "Whilst investigating the food of young fishes in general (Lebour, 1918—1919

—1920) some thousands of young clupeoids were examined with the result that by far the larger proportion of post-larvae were found to be empty . . ."

Contrary to Krogh's statement (*op. cit.*), none of Lebour's findings proves that fish larvae can and do obtain a sufficiency of such food particles as she described.

An exhaustive study of the biology of the Pacific sardine, *Sardinops caerulea*, has been undertaken since 1949 by the California Cooperative Oceanic Fisheries Investigations. In the course of this study, a vast amount of physical and biological data has been collected. With the specimens and data available, David K. Arthur of Scripps Institution of Oceanography is investigating the food relationships of the larvae of the sardine and some other species. According to Arthur's findings (orally communicated progress reports), sardine larvae less than 10 mm. in length feed primarily on the eggs and nauplii of copepods; they feed largely during daylight hours; the incidence of their feeding is very low.

The "low incidence of feeding" (i.e., among collections of larvae, one generally finds food organisms in the guts of only a very small percentage of the specimens) is apparent to, and remarked upon by, anyone who has spent much time in the study of marine fish larvae.

A number of theories could be reasonably advanced for this low incidence of feeding, but the fact remains that until it is positively explained, there is no justification for assuming that the stocks of larger, animate food particles are adequate to sustain larval populations.

Digestive rate.

Krogh (*op. cit.*) stated:— "In many transparent forms like larval fish the digestion is extremely rapid and the gut appears empty most of the time." The authority for this statement is apparently Lebour (1919—22 d: 458) who said:— "A probable reason for this apparent absence of food in the transparent stages is that the food must be very quickly digested on account of its being so conspicuous; thus it is probably taken only at long intervals and rapidly got rid of."

It is evident that Lebour was theorizing about the rate of digestion and did not present her statement as an established fact. There seems to be no evidence that digestion of the types of food described by Lebour is extremely rapid, and the fact that she was able to identify rather precisely so many of these food organisms would suggest the contrary (even if we grant that identification was made from those body parts of material such as chitin which could not reasonably be expected to be digested).

Among a large number of larval fishes held in the laboratory I have seen no indication that digestion proceeded at a very rapid rate, nor has it appeared to be very complete (i.e., digestion of such things as nauplii and veligers).

Nutrition of embryos.

Larval stages are still essentially embryonic in function and the successful development of embryos is predicated upon a sustained and immediately available supply of food. When the larval yolk is exhausted there is a period of time during which the larvae of most species of marine fishes are without food-storage tissues or organs which can sustain them for long. In many forms, reserves in such organs as the liver appear to be exhausted in a matter of hours.

Wunder (1936: 228—233), in discussing alimentary tracts of fishes, characterizes those of predacious habit as having a capacious stomach which enables them to pursue a "feast and famine" type of existence. On the other hand, fishes such as the cyprinids have no stomach and take their food in small amounts, frequently and regularly. Grossly, the position of the stomach in the very young larvae of many species of marine fishes is indicated only by the constriction of the pyloric valve. There can be no storage in the stomach, and whatever function the stomach may have in their digestive processes would have to be extremely rapid, because a food particle such as a nauplius passes from the mouth to below the pyloric valve in a matter of seconds. (Ingested nauplii of *Artemia* are still alive when they pass the pyloric valve of, for example, young larvae of the herring, *Clupea pallasii*.)

There is no evidence that marine fish larvae reduce energy requirements by becoming passive during the lengthy periods of time between particulate feedings. The fact that many larvae tend to rise to upper layers at night (when directive feeding is presumably of lowest incidence) suggests that activity is not suspended.

Organic matter in the sea.

One of the main arguments against Pütter's Theory was the prevalent belief that organic solutes are extremely dilute in sea water. Recognizing certain deficiencies in techniques used in the earlier work, Sverdrup *et al.* (1942: 249), in their discussion of Pütter's Theory, stated:— "Although the problem has attracted much discussion and speculation, there are very few trustworthy data concerning the amounts of carbon present in particulate or dissolved matter in the sea."

In examining the literature, one is almost forced to conclude that some of the participants in the controversy over Pütter's Theory were inclined, in discussing quantities and distribution of organic matter, to use data which favoured their particular beliefs. Not only the amounts of organic matter, but also the state to which the organic matter is subdivided, have apparently been misunderstood. The organic matter that has been referred to as "dissolved" by various authors has obviously included material of substantially different size categories, reflecting the manner in which water samples were treated and analysed. Techniques in sampling, filtering, centrifuging, and analysis of the organic matter have not yet been standardized. It is apparent that some early investigators testing Pütter's Theory failed to appreciate physical and biological processes (e.g., adsorption and microbial activity) which keep the organic system in constant flux, causing particular distortions of the natural picture when water samples are removed from the sea and taken into the laboratory. The actual composition of the inanimate organic constituents of sea water appears to have eluded difinition. And over all this, the natural variation in distribution and quality of organic matter, both living and dead, imposes a factor which has tremendously magnified the difficulties.

In spite of these many difficulties, one obtains the impression from the literature that there is a much greater amount of "dissolved" organic matter in the sea than exists in the particulate state. ZoBell (1946: 19) gives the ratios that have been found by different investigators as ranging from 1 : 7 to 1 : 4000 (particulate : dissolved).

As pointed out earlier, attention has for the most part been focused upon organisms of 40 to 50 μ in diameter or larger in the study of feeding habits of marine fish larvae. The ratios given above show that such organisms would probably constitute only an exceedingly small fraction of the organic matter present in a given body of water. Since feeding upon such organisms has appeared to take place so infrequently and irregularly, let us consider some of the other possibilities.

It is impossible for larvae to feed upon organisms larger than they can take into their mouths and swallow. Since the organisms to be found in the guts of larvae less than 10 mm. in length usually approach these limits, it seems that the material heretofore considered to constitute their diet might possibly represent only a small fraction of it, from the uppermost portion of the conceivable size range.

If such organisms as dinoflagellates and diatoms were taken to any appreciable extent, they would undoubtedly have been noted in the course of routine procedures of gut analysis. This is not the case, however, since such organisms are only rarely found in the larvae.

It is conceivable that nanoplankters such as bacteria and certain flagellates would be overlooked in routine gut analyses because of their small size and lack of colour. No extensive work has been done to determine the possible significance of such organisms in the diet of larval fishes.

Further down the size scale is the "dissolved" organic matter. Recent investigators using methods presumably more highly refined than those used by earlier workers have made some interesting observations.

Collier *et al.* (1950) described some organic matter that they have found as follows:— "The characteristics of the substance as it occurs in the natural sea water supply of this laboratory are as follows:— It passes bacteriological filters and is not thrown down by the ordinary laboratory centrifuge. The concentration in different samples ranges from 2 to 25 mg./l. and is extremely variable."

Fox *et al.* (1952) introduced the term "leptopel" and defined it as ranging from:— ". . . finely colloidal micelles to minute visible particles and including intimately associated micro-organisms such as bacterial cells, [which] will vary in quantity and in chemical constitution with reference to latitude, depth, season, and proximity to land."

Among a number of samples they found quantities of organic leptopel to vary from 0·25 to as high as 35·3 mg./l. Some of the material considered by Pütter (1909 b) appears to have consisted of this leptopel (rather than true solutes).

Although much remains to be determined regarding the suitability of dissolved organic matter as an energy source for marine organisms, certain fractions have been shown to be very important as growth factors (cf. Wilson, 1951). In such capacity, they profoundly affect distribution and survival of at least some higher forms of animals.

Utilization mechanisms.

The most serious objection to Pütter's Theory was based on the failure to find physiological mechanisms whereby dissolved nutrients could be concentrated and absorbed from dilute solution in natural waters. Regarding mechanisms, Krogh (1931) stated that at least one of two things must take place, (1) diffusion or (2) active transport. Pütter stressed the extent of surface area as the factor governing the amount of utilization of dissolved matter, and the two mechanisms considered by Krogh obviously refer to acquisition through the integument.

Direct simple diffusion through the integument under natural conditions would, as Krogh stated, be impossible because it would be directed against the concentration gradient. The permeability charcteristics of most integumentary processes cannot be expected to favour such diffusion, and mechanisms for the concentration and active transport of organic molecules through the integument have not been observed.

Other possible methods by which dissolved food materials might conceivably be gathered have not been sufficiently considered. A natural biological filter was described by MacGinitie (1945). The echiuroid worm, *Urechis caupo,* lives in a U-shaped burrow in the mud and pumps water through the burrow by peristalsis. The animal secretes a conical net of mucus which is open at the base, with the basal periphery attached to the burrow, and the apex of the cone attached around the anterior end of the worm. In such an arrangement, water pumped through the burrow must pass through the mucous net which strains out the food. After a period of pumping, the net with the food particles it has retained is eaten, and the process is repeated. MacGinitie found that the interstices of the net retained particles having a diameter of approximately 40 Å. Recognizing the adsorption that would take place on such a net and the progressive clogging of its interstices, we have here a mechanism that would enable the animal to concentrate and deliver to digestive surfaces molecularly divided materials of even smaller dimensions than the diameters of the net openings would imply.

While the mechanism found by MacGinitie is probably nothing like those sought by the earlier investigators, it is nevertheless a mechanism for utilizing the "dissolved" organic matter of sea water.

Collier *et al.* (*op. cit.*) found that the naturally occurring, filterable organic matter observed by them could induce oysters to pump when it was present in the water above certain threshold values (the threshold varied with temperature). These authors also found that an oyster would remove from 5 to 15 $^0/_0$ of the substance from the water passed through its body.

Although Collier *et al.* did not isolate the mechanism of collection, they demonstrated that one is present. Of equal importance is their demonstration of the presence of a mechanism with which the oyster detects and measures the amount of the organic substance in the water (the greater the carbohydrate concentration, the more water the oyster pumped).

Fox *et al.* (1953) demonstrated the ability of two representative filter feeders (one setous, the other ciliary and mucous) to collect by adsorption colloidally dispersed particles as small as vertebrate oxyhaemoglobin, i.e., 40 to 50 Å. The animals used in this demonstration were a mysid crustacean (not specifically identified) and the sea mussel, *Mytilus californianus.*

The feeding mechanisms of *Amphioxus* and tunicates were reviewed by Yonge (1928: 45—46). In these forms it has been seen that when water is passed over mucous tracts by ciliary action, food particles are caught by the mucus and carried into the digestive system. It would appear that the mucous tracts in these forms could pick up not only particulate matter but material in the colloidal and perhaps molecular size ranges as well.

Let us turn now to the condition in the larvae of some marine fishes.

The general understanding of osmoregulation in bony fishes began to emerge about 1930 (cf. Smith, 1932). It is now understood that "marine teleosts swallow relatively large quantities of sea water which subsequently undergoes absorption" (Smith, 1930: 501). The actual rate at which water must be swallowed depends in some degree upon the rate at which water is lost and salts gained through body surfaces, and hence upon the extent of those surfaces. It is interesting to remember in this connexion the fact that Pütter related the amount of dissolved nutrients taken up from the water to the extent of body surfaces, particularly gill areas (hence his stress upon benefits to organisms of small size). On several occasions bony fishes have been subjected to tests of Pütter's Theory, but aside from Pütter's original work, and the one individual fish considered by Moore *et al.* (1912), they have all been freshwater forms. Because of the reversal of the osmotic gradient (as compared with marine fishes), these species must avoid swallowing water. Hence, results of such tests on freshwater fishes cannot apply to marine forms. Discovery by an earlier investigator that freshwater fishes do not swallow water appears to have strongly influenced Pütter (1909 b: 210) in his conclusion that the alimentary tract was not the passage through which dissolved nutrients were being taken, even among marine fishes.

In marine teleosts we are dealing with forms in which rather large quantities of the surrounding medium are regularly taken into the alimentary canal and passed through the digestive surfaces. It is improbable that this water could contain enough dispersed organic matter to be significant in general nutrition. However, if there were some oral mechanism which could collect dispersed organic matter, then whatever water was swallowed might become nutritionally important.

In the course of my studies I have had occasion to examine histological sections of various body parts of the larvae of a few species. The isospondylid larvae examined are the anchovy, *Engraulis mordax,* the herring, *Clupea pallasii,* and the night smelt, *Spirinchus starksi.* Although larvae of the anchovy are only about half the size at hatching of those of the other two species (i.e., *ca.* 3 to 4 mm. and *ca.* 7 to 8 mm. total length, respectively), all three are morphologically similar and during early stages of development the histological conditions of the three compare favourably. Since I have studied the smelt more than either of the other two species, it will be used for reference in the following discussion.

Mucous cells which line the esophageal tract extend forward over the roof and floor of the buccal cavity. When the mouth is distended its floor bulges posteriorly, forming a lateral pouch on either side, at the back of the gill openings. Upon closing, the floor and roof of the mouth are brought tightly together. Although no cilia were found in the mouths of several species examined, musculature across the roof and floor keeps the mucus moving posteriorly in regular, peristaltic waves.

It would appear that by adsorption and simple adhesion, these mucous tracts could easily collect the "dissolved" organic matter from water taken into the mouth.

The capacity of the mouth of this larva is about 0·04 μl. Under *laboratory* conditions, in water of 14° to 15°C., and with 95 $^0/_0$ of oxygen saturation, the *minimal* rate at which this animal refills its mouth in respiring is about 20 times per minute. At this rate, it would pass across these mucous surfaces about 1·15 ml. of water in the course of 24 hours or 11·5 ml. in a period of 10 days.

The nature of the "dissolved" organic matter that the larva might glean by this mechanism remains an open question. Even with regard to quantity we have no figures based on samples from waters which are known to be supporting populations of such larvae. Arbitrarily, let us take the figures of Krogh (1931: 439):— "Dissolved organic substances are present in fairly large quantities, 10 mg. per litre or more, with a combustion value of 40 cal. per litre or more in most fresh waters. The quantities in sea water appear to be of the same order of magnitude."

In such a solution, the mucous surfaces discussed above would be exposed to not less than 0·11 mg. of "dissolved" organic substances during a period of 10 days. This is an admittedly small figure, but such a quantity might be important in the economy of this larva, whose *wet* weight is calculated to be no more than 0·9 mg.

The condition described in *Spirinchus starksi* is similar to that found in *Amphioxus* and the tunicates discussed by Yonge (*op. cit.*). The musculature effecting respiration and peristalsis in fish larvae appears to be a mechanism similar for all practical purposes to the cilia of the tunicates in bringing food material into contact with mucous collecting surfaces.

The condition in *Spirinchus starksi* (also in *Clupea pallasii* and *Engraulis mordax*) contrasts sharply with that in such forms as the atherinids. In the young larvae of *Atherinopsis californiensis* less than 10 mm. long, the mucosa is confined to the constricted portion of the esophagus and needle-like teeth are found on the tongue and roof of the mouth. Atherinids can be reared in the laboratory with relative ease, and prosper on a diet of particulate matter such as nauplii — a diet that appears to leave much to be desired in so far as food for such forms as *Spirinchus* is concerned.

Acknowledgement.

I wish to thank Drs. Joel W. Hedgpeth and Denis L. Fox for valuable comments on the manuscript.

Summary.

It is the general opinion that early larval stages of marine fishes feed almost exclusively upon invertebrates whose sizes range upwards from 40 to 50 μ in diameter. About 45 years ago August Pütter concluded that aquatic organisms depended heavily upon organic nutrients in solution in the water. In testing Pütter's Theory other workers have, for the most part, concluded that dissolved organic constituents of natural waters could be of little significance in general nutrition of higher animal forms. Among the subjects of Pütter's experiments were five species of marine teleosts. Since his original work, only one individual marine fish has been subjected to a test of Pütter's Theory, and this work was done over 40 years ago.

Among marine fish larvae the incidence of feeding (upon the organisms which have been believed to constitute their diets) is extremely low. Since so many larvae collected from nature have guts in which there is no trace of food (as seen in ordinary microscopy), it has been assumed by some that digestion is very rapid. There is no direct evidence for this.

Larval stages are essentially embryonic and it seems illogical to assume that their survival could depend on the "feast and famine" type of existence that a low incidence of feeding would imply. Several aspects of the matter of the very finely divided and dissolved organic substances in the sea have not been brought into sharp focus. Recent studies by other investigators indicate that there may be sufficient quantities of the "dissolved" organic matter (leptopel) to constitute an important factor in nutrition of some aquatic animals. The early larval stages of some marine fishes have an extensive layer of mucous cells over the surfaces of the back of the mouth. Rates at which water is pumped through the mouth during respiration indicate that the mucosa might serve as a mechanism for collecting important quantities of dispersed organic matter of a nature that would have been overlooked

in the course of the routine gut analyses conducted in the past. Marine teleosts swallow rather large quantities of water, which freshwater fishes do not; therefore results of tests conducted on freshwater forms cannot apply to marine species.

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RACES OF THE STRIPED BASS, *Roccus saxatilis* (WALBAUM), IN SOUTHEASTERN UNITED STATES

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RACES OF THE STRIPED BASS, *Roccus saxatilis* (WALBAUM), IN SOUTHEASTERN UNITED STATES

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A knowledge of the origin of the stock or stocks exploited in a fisheries is basic to sound management. A study to determine the racial structure of Atlantic Coast striped bass is under way and recent investigations of southeastern stocks have produced tentative concepts. The results should be considered preliminary because specimens from too few year classes are available for study. As used here the term "race" implies a lower level of differentiation than that of a subspecies.

The major published findings concerning racial problems to date are as follows: Merriam (1937 and 1941) and Vladykov and Wallace (1938) showed that some Chesapeake Bay striped bass, two years and older, undertake a non-spawning coastal migration northward in the spring. In the fall they return to Chesapeake Bay by approximately the same route although some migrants may enter and winter over in northern coastal rivers. Vladykov and Wallace (1952) indicated that different sub-races may make up the Chesapeake Bay race although adequate substantiating data are not presented. Raney and de Sylva (1953) showed that fin-ray counts in young striped bass were lower in samples from the Hudson River than those from Chesapeake Bay. The degree of differentiation was approximately 80 per cent, based on a character index combining dorsal, anal, and total pectoral soft-ray counts. They also suggested that the Hudson River may contain an upstream and a downstream population. Raney, Woolcott, and Mehring (1954) concluded that (a) the Hudson River race migrates to the western quarter of Long Island Sound and the region near the mouth of the Hudson River including the northeastern New Jersey shore and the south shore of Long Island east to Jones Beach; (b) fin-ray counts of young of the 1953 year class confirmed the findings based on other year classes concerning the racial separation of Chesapeake and Hudson River striped bass; (c) in fin-ray counts, samples from Rhode Island and northward are close to the Chesapeake race; (d) although shifts in the fin-ray counts occur from year to year the change is slight compared to the degree of differentiation between races and usually has little effect on the percentage of separation; and, (e) Albemarle Sound samples differ from South Carolina series in lateral-line scale counts.

MATERIAL

Samples from Albemarle Sound were mostly young of several year classes but include some juvenile and adult specimens. Those from the Santee-Cooper River, South Carolina, were mostly young (Lake Marion) and yearlings of the 1954 and 1953 year classes which were made available by George D. Scruggs, Jr. and Jefferson C. Fuller, Jr., of the South Carolina Wildlife Resources Department. Prior to this, our South Carolina sample consisted of only ten young and small adults which were loaned by E. Milby Burton and Albert Schwartz of the Charleston Museum. An adequate sample of adult striped bass from the St. Johns River system in eastern Florida was counted during September 1954 by William M. McLane of the Florida Game and Freshwater Fish Commission and the authors. Only four specimens of striped bass have been examined from the Gulf of Mexico drainages of Florida and Mississippi. It is hoped that additional specimens will be

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[2] Recipient of a Sport Fishing Institute Fellowship, 1953–54.

Corrections to be made in Races of the Striped Bass, *Roccus saxatilis* (Walbaum) in Southeastern United States by Raney, Edward C. and William S. Woolcott, 1955. Journ. Wild. Manag., vol. 19(4), Oct. The correct number or word is underlined.

Page 445. Table 1, eighth line under "Locality" should read as follows:

"S.C.,Lake Marion 1 *1* 4 9 14 24 25 41 39 *23* 20 9 4 .. .. .. 2*14* 59.*1* 7*4*"

All tables under "Locality": Lake Moultrie, Cooper River, and Ashley and Edisto R. which are in South Carolina should have been indented one space only. They are not tributaries of Lake Marion, as are Wyboo Cr., Eutaw Sp. and Wilkinson Ld.

P. 446. In second column under "FIN-RAY COUNTS": end the first sentence with "southward"; viz. delete "*except for the inadequate sample.....*"

P. 446. Table 2: the last line should read:

"West Fla. and Miss. .. .. .. *1* *3* .. .. 4 *10.0* *25*"

P. 447. Delete the last sentence in the second paragraph which reads: "*The West Florida-Mississippi sample......*"

P. 447. Table 4, the last line should read:

"West Fla. and Miss. .. ..2 2 .. .. 4 *33.5* *0*"

Also, the last number in the line immediately above is *4* rather than 0.

P. 448. Revise the second complete sentence so that it reads: "The St. Johns River, Florida population differs significantly from the South Carolina and Albemarle samples."

P. 448. Table 5, the last line should read:

"West Fla. and Miss. .. .. 1 1 2 .. .. 4 *56.2* *25*"

P. 449. In the next to last paragraph in the second column add the word "scale" so that the sentence reads "Counts of the relatively few and inadequate samples from West Florida and Mississippi give indications of significant *scale* differences."

le available by Gulf Coast fishery biolos. The localities in South Carolina reed to below are shown in Figure 1.

Characters Studied

'in-ray and lateral-line scale counts of ng have been emphasized to date. Body portions and scale structure may show erences from place to place but there are few large specimens in our collections prove this.

Results

.ateral-line scale counts are shown in ole 1 and illustrated for southern samples 'igure 2. Northern stocks may differ from h other on a low level. Frequency disoutions approximate the normal except the Hudson and Cooper rivers where types seem to be present. The Albemarle ind sample differs on a relatively high el from the South Carolina composite nple; the average separation is 76 per cent en a line is drawn between 60 and 61 les (see Ginsburg, 1938). The St. Johns 'er, Florida, sample averages lower than composite South Carolina sample; 85 cent average separation is obtained when ne is drawn between 56 and 57 scales. The Johns River sample is separated 93 per cent on the average from the Albemarle Sound sample.

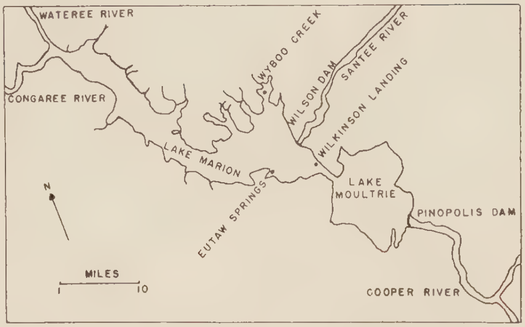

Fig. 1. Outline map showing collecting stations in the Santee-Cooper reservoir system, South Carolina.

An examination of the South Carolina samples indicates that two stocks may be present. One is represented by the four samples from Lake Marion and a small sample from Lake Moultrie. Here the lateral-line counts are relatively high, usually 58 to 60. Samples within Lake Marion, which consisted only of young of the 1954 year class, differ somewhat from place to place as did samples taken at the same locality (Wilkinson Landing) at different times (Fig. 2). It is to be noted that these differences are not significant.

BLE 1.—Frequency Distribution of Lateral-Line Scales in Striped Bass. The Last Column (%) Indicates the Percentage of Specimens With 60 or Fewer Scales

	Lateral-Line Scales																		
Locality	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	No.	Mean	%
Lawrence R.	..	..	..	..	..	4	7	11	14	16	14	14	17	2	..	..	99	61.3	36
v Brunswick	..	..	1	1	4	3	12	16	29	20	25	14	7	6	6	..	144	60.9	46
ɔde Island	..	..	..	..	1	4	2	5	9	10	12	13	4	7	1	1	69	61.6	30
dson River	..	..	1	2	5	6	8	10	6	13	8	2	3	1	..	..	65	59.6	58
aware River	..	..	..	..	..	..	2	4	9	19	17	10	12	5	3	2	83	62.2	18
esapeake Bay	..	1	..	2	9	14	14	26	31	27	33	13	8	2	..	..	180	60.1	54
., Albemarle Sound	..	..	..	..	..	..	2	4	6	11	8	3	3	4	2	..	43	61.7	28
., Lake Marion	1	..	4	9	14	24	25	41	39	33	20	9	4	..	..	..	223	59.2	70
Vyboo Cr.	..	..	1	4	4	9	12	16	23	11	11	7	3	..	..	..	101	59.6	68
utaw Sp.	1	..	..	1	3	2	2	4	3	3	1	2	1	..	..	..	23	59.0	70
Vilkinson Ld.																			
Sept. 10	..	1	2	4	7	9	9	16	10	5	5	..	..	..	..	..	68	58.3	85
Sept. 27	..	..	1	..	..	4	2	5	3	4	3	..	..	..	..	..	22	59.2	68
ake Moultrie	..	..	..	2	..	1	1	1	2	1	1	1	..	..	..	..	10	59.9	70
ooper River	1	5	7	5	9	5	11	11	7	..	..	..	..	..	..	..	61	56.8	100
shley and Edisto R.	1	1	..	4	..	..	1	..	1	..	..	..	..	..	..	..	8	55.4	100
., St. Johns R.	4	4	8	4	3	1	1	..	..	..	..	..	..	..	..	..	25	54.2	100

ounts on St. Lawrence samples furnished by V. D. Vladykov.

A down-river population seems to be represented by the composite sample from the Ashley and Edisto rivers, which, unfortunately, is small and which represents juvenile and small adult specimens not of the same year class as the Cooper River or Lake Marion samples. The Cooper River sample, which consists of juvenile and adult specimens, is intermediate between the Lake Marion population and the South Carolina Coastal Plain population. It also shows a bimodal distribution (Table 1). These specimens were taken below Pinopolis Dam and seem to represent both spawning migrants from downstream and Lake Marion bass which perhaps came downstream through the navigation locks. The lowland or Coastal Plain population of South Carolina appears to occupy an intermediate position in lateral-line scales between the Cooper River and St. Johns River, Florida populations.

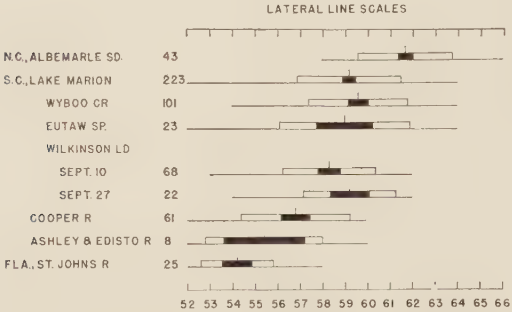

FIG. 2. Lateral-line scale counts of striped bass. For each locality the range of variation is shown by a heavy horizontal line, the mean by a vertical line. The blackened part of each bar comprises two standard errors of the mean on either side of the mean. One-half of each black bar plus the white bar at either end, outline one standard deviation on either side of the mean. Considerable reliance can be placed on the significance of the difference between samples if the corresponding black bars are separated or only slightly overlap. Method of representation adapted from Hubbs and Hubbs (1953: 51).

A cline is observable in the distributions shown in Figure 2; they vary from low counts in the south to high counts in the Albemarle Sound samples. No cline is represented by our samples from north of Albemarle Sound.

FIN-RAY COUNTS

Anal-ray counts are given in Table 2. There seems to be little difference in anal-ray counts in samples from Albemarle Sound and southward except for the inadequate sample from west Florida and Mississippi which have 10 rather than 11 anal rays. The numbers of anal rays seem rather stable except perhaps for the New Brunswick, Canada, sample. The upper Hudson River race also has a low average.

Dorsal-ray counts are given in Table 3.

TABLE 2.—NUMBER OF ANAL SOFT RAYS IN STRIPED BASS. THE LAST COLUMN (%) GIVES THE PERCENTAGE OF SPECIMENS WITH 10 OR FEWER RAYS

Locality	Anal Rays 7	8	9	10	11	12	13	No.	Mean	%
St. Lawrence River	..	..	..	21	79	..	..	100	10.8	21
New Brunswick	1	1	13	61	66	1	1	144	10.4	53
Nova Scotia	..	..	..	..	39	..	..	39	11.0	0
Hudson River (upper)	..	..	8	107	142	3	..	260	10.6	44
Delaware Bay	..	..	2	46	190	2	..	240	10.9	20
Chesapeake Bay	.	..	..	124	825	3	..	952	10.9	13
N.C., Albemarle Sound	..	..	..	4	56	..	..	60	10.8	10
S.C., Lake Marion	..	..	.	6	218	1	..	225	11.0	3
Wyboo Cr.	..	..	..	3	98	..	..	101	11.0	3
Eutaw Sp.	..	..	..	..	23	..	..	23	11.0	0
Wilkinson Ld.										
Sept. 10	..	..	..	3	64	1	..	68	11.0	4
Sept. 27	..	..	..	..	25	..	..	25	11.0	0
Lake Moultrie	..	..	..	..	8	..	..	8	11.0	0
Cooper River	..	..	..	7	55	..	..	62	10.9	11
Ashley and Edisto R.	..	..	..	1	7	..	..	8	10.9	13
Florida, St. Johns R.	..	..	..	1	22	2	..	25	11.0	0
West Fla. and Miss.	..	..	1	3	..	..	..	4	9.8	100

e count is modally 12 in the geographic a between Albemarle Sound and Missis- pi. A slight difference is found in com- ing those from Lake Marion with those m Cooper River below Pinopolis Dam. e Hudson River race is unique; samples ve 11 rather than 12 as the modal number.

The total pectoral-ray counts are shown Table 4 and in Figure 3. There is an in- ation of population differentiation within the Santee-Cooper River system in this character; the upstream population has the higher count. The St. Johns River, Florida, population has the highest count found along the Atlantic Coast and approaches the values for New Brunswick and Nova Scotia samples. The west Florida-Mississippi sample yielded a low count, the lowest found in any sample of striped bass.

For the most part the fin-ray counts vary

BLE 3.—Number of Dorsal Soft Rays in Striped Bass. The Last Column (%) Gives the Percentage of Specimens With 11 or Fewer Rays

Locality	Dorsal Rays								
	9	10	11	12	13	14	No.	Mean	%
Lawrence River	..	1	30	69	..	..	100	11.7	31
w Brunswick	..	10	17	124	1	..	144	11.9	13
va Scotia	..	..	1	38	..	..	39	12.0	3
dson R. (upper)	2	24	183	38	1	1	249	11.1	84
laware Bay	..	6	99	128	7	..	240	11.6	44
esapeake Bay	..	7	248	687	8	1	951	11.8	27
C., Albemarle Sound	..	..	9	51	..	..	60	11.8	15
., Lake Marion	..	..	70	146	1	..	217	11.7	32
Vyboo Cr.	..	..	28	73	..	..	101	11.7	28
Eutaw Sp.	..	..	5	18	..	..	23	11.8	22
Vilkinson Ld.									
Sept. 10	..	.	27	40	1	..	68	11.6	41
Sept. 27	..	..	10	15	..	..	25	11.6	40
Lake Moultrie	..		4	12	..	..	16	11.8	25
Cooper River	..	5	16	40	1	..	62	11.6	34
Ashley and Edisto R.	..	..	..	8	..	..	8	12.0	0
rida, St. Johns R.	..	..	2	23	..	..	25	11.9	1
st Fla. and Miss.	..	..	..	4	..	..	4	12.0	0

BLE 4.—Number of Pectoral Rays (Both Sides) in Striped Bass. The Last Column (%) Gives the Percentage of Specimens With 32 or Fewer Rays

Locality	Pectoral Rays														
	27	28	29	30	31	32	33	34	35	36	37	38	No.	Mean	%
w Brunswick	..	..	..	..	..	13	14	112	5	..	..	..	144	33.8	9
va Scotia	..	..	..	..	..	3	7	25	4	..	..	..	39	33.8	8
dson R. (upper)	..	2	7	14	29	134	33	36	1	..	..	..	256	32.1	73
laware Bay	..	..	4	..	18	55	53	73	29	2	..	..	234	33.1	33
esapeake Bay	1	4	6	23	27	182	168	406	75	37	6	1	936	33.4	26
C., Albemarle Sound	..	..	..	..	..	26	10	24	..	..	..	..	60	32.9	43
., Lake Marion	..	..	1	..	8	35	43	120	9	1	..	..	217	33.4	20
Vyboo Cr.	..	..	..	..	4	15	16	60	6	..	..	..	101	33.5	19
Eutaw Sp.	..	..	..	..	1	1	4	17	..	..	..	..	23	33.6	8
Vilkinson Ld.															
Sept. 10	..	..	1	..	2	13	18	32	1	1	..	..	68	33.2	23
Sept. 27	..	..	..	..	1	6	5	11	2	..	..	..	25	33.3	28
ake Moultrie	..		..	..	..	2	8	..	..	..	..	..	10	32.8	20
Cooper R.	..	..	1	1	2	25	17	14	1	1	..	..	62	32.7	47
shley and Edisto R.	..	..	..	..	1	4	..	3	..	..	..	..	8	32.6	63
., St. Johns R.	..	..	..	..	..	1	4	16	1	2	..	..	24	34.0	0
st Fla. and Miss.	..	..	..	..	2	2	..	..	..	..	..	..	4	31.8	100

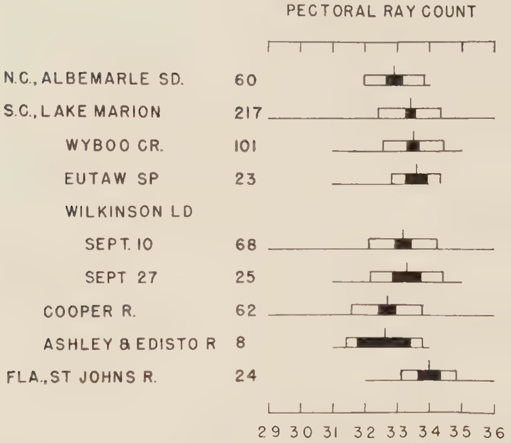

Fig. 3. Total pectoral-ray counts of striped bass.

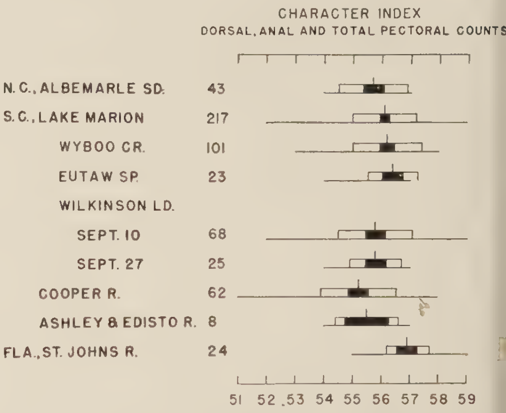

Fig. 4. Character indices for samples of striped bass. The index was obtained by adding dorsal, anal, and total pectoral soft rays.

in the same direction and an index formed by adding anal, dorsal, and pectoral soft rays gives a total picture of the trend (Table 5, Figure 4). The Albemarle Sound and the composite South Carolina population do not differ significantly. The St. Johns River, Florida population differs from the west Florida-Mississippi population; each apparently represents an extreme trend. Both differ significantly from the South Carolina and Albemarle samples. Within the Santee-Cooper River system, South Carolina, there seems to be an indication of two different populations. The upstream population has the higher index.

Discussion

In view of the differentiation in lateral-line scales found in the North Carolina, South Carolina, and east Florida stocks it seems pertinent to consider the possible causes of these differences. The authors favor

Table 5.—Frequency Distribution of the Character Index (Sum of Dorsal, Anal, and Pectoral Soft Rays) in Striped Bass. The Last Column (%) Indicates the Percentage of Specimens With an Index of 55 or Less

Locality	Character Index																	
	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	No.	Mean	%
New Brunswick	..	..	..	..	..	2	4	11	22	50	48	7	..	..	..	144	56.0	23
Nova Scotia	..	..	..	..	..	..	..	..	3	8	24	4	..	..	..	39	56.7	8
Rhode Island	..	..	..	..	1	..	..	5	12	16	26	4	2	1	..	67	56.3	27
Hudson River	..	..	1	5	13	27	49	74	59	23	22	1	..	..	..	274	54.0	83
Delaware River	1	..	..	..	1	1	4	15	15	18	18	9	1	..	..	83	55.6	45
Chesapeake Bay	..	..	..	..	1	5	9	25	80	127	219	55	27	2	1	551	56.4	22
N.C., Albemarle Sound	..	..	..	..	..	..	2	4	12	11	14	..	..	..	..	43	55.7	42
S.C., Lake Marion	..	..	..	..	..	1	6	13	40	68	81	7	1	..	..	217	56.1	28
Wyboo Cr.	..	..	..	..	..	..	4	6	13	27	46	5	..	..	..	101	56.2	23
Eutaw Sp.	..	..	..	..	..	..	..	1	3	5	14	..	..	..	..	23	56.4	17
Wilkinson Ld.																		
Sept. 10	..	..	..	..	..	1	2	3	19	24	16	2	1	..	..	68	55.8	37
Sept. 27	..	..	..	..	..	..	..	3	5	12	5	..	..	..	..	25	55.8	32
Lake Moultrie	..	..	..	..	..	..	..	..	1	3	4	..	..	..	..	8	56.4	13
Cooper R.	..	..	..	..	1	1	5	11	18	14	10	2	..	..	..	62	55.2	58
Ashley and Edisto R.	..	..	..	..	..	..	..	1	4	1	2	..	..	..	..	8	55.5	62
Florida, St. Johns R.	..	..	..	..	..	..	..	..	1	6	12	4	1	..	..	24	56.9	4
West Fla. and Miss.	..	..	..	..	..	..	1	1	2	..	..	..	..	..	..	4	54.3	100

e hypothesis that scale counts and fin-ray aracters are genetically fixed in striped ss but may fluctuate within a narrow nge in response to environmental changes, ch as temperature, at the time these charers are determined in the embryo. Exrimental evidence to date (see Tåning, 52, for references) with other fishes usually licates an increased number of parts with ver water temperatures. The data on eral-line scale counts (Table 1) show a adual or clinal increase from St. Johns ver, Florida northward to Albemarle und. However, no such cline is noted in mparing samples from Chesapeake Bay to e St. Lawrence River, an area which cernly experiences varied temperature conions. An increase occurs in an upstream ection within the Santee-Cooper River stem. A slight decrease is noted upstream the Hudson River.

Under experimental conditions, fin-ray ints normally shift in the same direction do lateral-line scales; a higher number at ver water temperatures. Where differences occur in fin-ray counts in the region from e St. Johns River, Florida, to Albemarle und, a reverse trend, a slight decrease vard the north, exists. Within the Santeeoper River system there is a slight inase in an upstream direction. Perhaps e water temperatures at spawning time e lower downstream below Pinopolis Dam. stream in the Hudson River the number dorsal rays definitely decreases.

For the most part critical temperature a at spawning time are lacking so that do not know that shifts in the fin-ray l scale counts in the striped bass are related with temperature. Furthermore, nature spawning does not usually occur striped bass until a threshold temperature about 58°F. is reached. The incubation iod is short; 48 hours at 64.2°F. (Pearson, 38: 831). The "supersensitive" period en the embryo is especially sensitive is known but is likely to be of short dura-n, seemingly a matter of hours. It seems bable that widely separated populations striped bass along the Atlantic Coast may dergo early development at about the same ter temperature. Pronounced changes in nperature due to sudden storms might se shifts which could result in an unusual tribution of counts for part of a year class. ch differences would tend to balance out if samples including several year classes were used. These problems may be clarified by researches to be carried on over the next three years.

Whether the cause of the differences which have been found to exist is primarily genetic, or is a result of environmental modification of the phenotype, makes relatively little difference as long as the variations in a given area are approximately the same from year to year. To date, an insufficient number of year classes of striped bass have been studied from the southeastern United States, but in the Hudson River where studies have been made of several year classes since 1949 relatively small differences in counts have been noted from year to year.

The meristic data presented here, which indicate an upstream versus a downstream population in the Santee-Cooper River system, South Carolina, are strengthened by the findings of Scruggs and Fuller (1955) regarding migration within the river system. It is assumed that the Lake Marion stock was derived from an upriver stock which had already been differentiated much as has the upstream Hudson River race. When the rivers were dammed, the upstream form apparently found a suitable habitat and now represents a fishery of great potential value.

Samples of striped bass from many coastal areas where populations are known to occur are still lacking, and a future study of material from several Georgia rivers, as well as other waters in North and South Carolina, will further clarify the picture of racial structure of the stocks. Counts of the relatively few and inadequate samples from west Florida and Mississippi give indications of significant differences. There is little chance that there has been gene exchange between these and Atlantic populations since the emergence of the Florida peninsula from the seas.

SUMMARY

It is tentatively concluded that the South Carolina stock of striped bass is an endemic race which in turn is differentiated into an upstream form which may not go to the sea and a downstream form which at least goes downstream to brackish water. Certainly there is little interchange between South Carolina stock and that of Albemarle Sound, North Carolina, or the St. Johns River, Florida. The latter is a good race but its relationships with populations immediately to the north in Georgia rivers are unknown.

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Length-Weight Relationship in Migrating Fry of Pink Salmon (*Oncorhynchus gorbuscha*) in Sashin Creek, Little Port Walter, Alaska

BERNARD EINAR SKUD

THE spawning migration of pink salmon, *Oncorhynchus gorbuscha* (Walbaum), at Sashin Creek, Little Port Walter, Alaska occurs during the months of August and September. Length measurements show that adult females passing through the counting weir early in the fall are larger than females in the later portion of the run. The seaward migration of the fry takes place during the months of March, April and May. If, as biologists believe, early and late migrating fry are the progeny of early and late adults, respectively, a similar trend in size might be expected. The purpose of this research is to determine whether earlier fry migrants are larger than the late migrants, and thus have a better chance of survival.

In 1941 and 1942 at Sashin Creek the numbers of migrating fry were so great that it was not feasible to count each individual. Instead the number of pints of migrants was counted and an actual count of the number of fry per pint was made on various days during the season. Although there was a random fluctuation in these numbers per pint, a positive correlation was found between the numbers and the time of migration. There is a general increase in the number of fry per pint which indicates a decrease in size as the migration progresses (Tables I and II). Using the 20th sampling day as an arbitrary mid-point, the mean numbers of fry per pint in the early and late portions of each season were compared. ("Students" t for 1941 $= 1.60$, 14 d.f., $P = 0.14$; 1942 $= 3.29$, 11 d.f., $P < 0.01$.)

In order to make a detailed comparison of individuals or groups of individuals in a specific run of fry migrants, use is made of the length-weight relationship $W = aL^n$, where W is the weight in grams, L the fork length in mm., and a and n are empirically determined constants (Lagler, 1952).

The values of log a and n were determined for a time-scaled series of samples in 1942, 1943, 1944 and 1948, the only years when fry sampling included individual length and weight measurements. The samples were taken from the downstream weir at the mouth of Sashin Creek. Sampling periods were spaced throughout the downstream migration so that samples provided data on successively later migrants. The values of log a and n for each sampling period are presented in Table III.

To validate the use of an analysis of covariance, tests were applied to determine normality and constant variance of log W. These tests were applied only to the data for 1942, when samples were large enough to show significant results. In the majority of cases, log W was normally distributed for each length class and the variance was constant from length to length. Since the general assumptions of analysis of covariance were fulfilled, the usual test was applied and the slopes of the lines were found to be significantly different at the 5 percent level.

Log a and n generally increase in value as the seaward migration progresses (Table III). To measure the probable occurrence of the trend, use is made of the time-series significance tests based on signs of differences and the table

TABLE I

COMPARISON OF THE NUMBER OF FRY PER PINT AND SUCCESSIVE SAMPLING DAYS AT SASHIN CREEK IN 1941 (COEFFICIENT OF CORRELATION = +.66)

Date	Number of days from first sampling	Number of fry per pint
March 17	1	971
24	8	973
27	11	1650
30	14	1607
31	15	1742
April 2	17	1741
2	17	1808
3	18	1670
5	20	1798
7	22	1559
9	24	1730
9	24	1720
12	27	1681
18	33	1807
20	35	1674
24	39	1800

of probability presented by Moore and Wallis (1943). The probabilities of the directional movement of log *a* and *n* for each year are presented in Table IV.

Though only three of the independent tests are significant, the aggregate suggests that the probabilities on the whole are lower than would have been obtained by chance. Using Fisher's

TABLE II

COMPARISON OF THE NUMBER OF FRY PER PINT AND SUCCESIVE SAMPLING DAYS AT SASHIN CREEK IN 1942 (COEFFICIENT OF CORRELATION = +.81)

Date	Number of days from first sampling	Number of fry per pint
April 7	1	1441
8	2	1481
9	3	1554
19	13	1594
21	15	1473
22	16	1562
23	17	1521
28	22	1562
29	23	1557
May 6	30	1678
7	31	1607
13	37	1625
14	38	1657

TABLE III

VALUES OF LOG *a* AND *n* OF SUCCESSIVE FRY SAMPLES FROM SASHIN CREEK, LITTLE PORT WALTER

Year	Date	Number in sample	log *a*	*n*
1942	March 14	50	−2.296	1.118
	March 23–24	110	−2.704	1.392
	March 25–27	100	−3.436	1.879
	April 2–3	110	−3.746	2.080
	April 9–10	120	−4.125	2.328
	April 16–17	120	−4.501	2.574
	April 23–24	120	−4.309	2.445
	April 30, May 1	120	−4.524	2.576
	May 7–8	120	−4.911	2.835
	May 14–15	120	−4.475	2.536
1943	April 29, May 3	100	−2.851	1.495
	May 6–10	100	−3.115	1.991
	May 17–20	100	−3.716	2.062
	May 24–31	100	−3.891	2.173
	June 3–7	100	−3.540	1.935
1944	March 26–27	96	−3.610	2.007
	April 2–3	94	−4.417	2.535
	April 9–10	100	−3.173	1.703
	April 16–17	100	−3.482	1.899
	April 25–26	100	−3.484	1.897
	May 1–2	100	−3.518	1.924
	May 8–9	100	−4.218	2.382
	May 15–16	100	−4.249	2.390
1948	May 4	50	−5.451	3.186
	May 10	50	−5.301	3.074
	May 17	50	−3.411	1.813
	May 24	100	−4.046	2.243
	May 31	50	−4.455	2.506

TABLE IV

PROBABILITY OF TREND OF LOG *a* AND *n* AS DETERMINED FROM TIME SERIES SIGNIFICANCE TESTS BASED ON SIGNS OF DIFFERENCES (MOORE AND WALLIS, 1943)

Year	P of log *a*	P of *n*	Number of samples
1942	.026	.026	10
1943	.450	.450	5
1944	.012	.225	8
1948	1.000	1.000	5

TABLE V

ESTIMATED LOG OF THE WEIGHT AT DIFFERENT LENGTHS IN 1942 AT SASHIN CREEK, ALASKA*

Date	Length in millimeters								
	27	28	29	30	31	32	33	34	35
Mar. 14	−.695	−.677	−.660	−.644	−.628	−.612	−.597	...	...
Mar. 23–24	...	...	...	−.647	−.677	−.608	−.590	−.572	...
Mar. 25–27	...	...	−.688	−.661	−.634	−.608	−.583	−.559	...
Apr. 2–3	...	...	−.703	−.673	−.643	−.614	−.587	−.560	−.533
Apr. 9–10	...	...	−.720	−.685	−.652	−.620	−.589	−.559	−.530
Apr. 16–17	...	−.776	−.737	−.699	−.662	−.627	−.592	−.559	−.527
Apr. 23–24	...	−.770	−.733	−.697	−.662	−.628	−.596	−.564	−.533
Apr. 30, May 1	...	...	−.757	−.719	−.682	−.647	−.612	−.579	−.546
May 7–8	...	...	−.765	−.723	−.683	−.644	−.606	−.569	−.533
May 14–15	...	−.806	−.767	−.730	−.693	−.659	−.625	−.592	−.560

* Log *W* is presented only for the lengths within the range for a given sample.

(1944) method for combining probabilities from tests of significance, the probability of the combined values in Table IV is found to be .020.

Estimates of the logarithm of the weight at the different lengths in each sample are determined from:

$$n\ (\log L) + \log a = \text{estimated} \log W$$

Table V shows the estimate log *W* for the samples taken in 1942. The consistent negative increase of log *W* for each length class indicates a decrease in weight as the season progresses.

A regression diagram combining the data on a monthly basis and using the empirical weights of each individual (Fig. 1) exemplifies the phenomenon that, for a given length class, the weight of early migrants is greater than the weight of late migrants. Thus, fry migrating seaward in the spring of the year do exhibit the same trend in size as adults during their spawning migration at Sashin Creek.

The importance of the size phenomenon to the early life history of the species warrants further discussion. Neave (1948) pointed out that factors which reduce the growth rate can be expected to have an unfavorable effect on survival, and Brett (1952) showed that the mortality of young salmon due to low temperatures was greater among smaller individuals. At Sashin Creek, then, chances of survival may be more favorable for the early, larger fry than for the later and smaller migrants.

Possible factors which produce the length-weight difference between early and late fry migrants fall in three general categories—environmental, physiological and genetic. The listing which follows is not considered to be exhaustive.

I. Environmental.

1. Earlier egg deposition may be more favorably synchronized with climatological

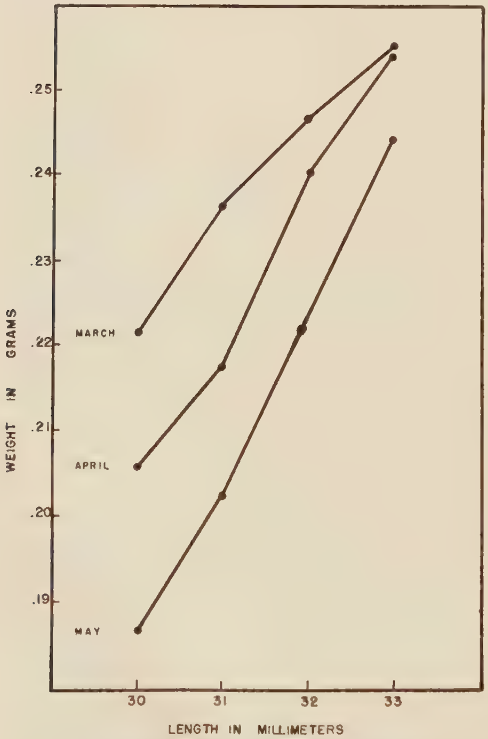

Fig. 1. Comparison of the averages of the empirical weights for given lengths during March, April and May of the 1942 migration at Sashin Creek.

changes during incubation. Low temperatures in the fall may have an adverse effect on eggs from a late deposition, whereas, eggs of earlier deposition in a more advanced stage of development may be less susceptible to such conditions.

2. At Sashin Creek, early adults usually utilize the upper reaches of the spawning area and the resulting progeny have a greater distance of stream to travel before reaching the sampling station. These individuals are exposed to more predators than are fry hatched in the lower reaches of the stream, and the existence of selective predation could result in a biased size distribution at the counting station.
3. Reports suggest that fry do not feed in fresh water, but this theory has not been proven and the possibility of feeding differences between the fry should be entertained.

II. Physiological.

1. Differences of nutritive values within the eggs of early and late individuals may exist, and similarly, the rate of yolk absorption may differ.
2. A shorter incubation period could well be responsible for the more favorable growth in early migrants. Increased metabolism may institute more complete utilization of available nutrients.
3. The later migrants may remain in the stream following emergence for a longer period than the early migrants, and this could be adverse to their best growth.

III. Genetic.

1. Data gathered from Sashin Creek show that in six out of seven years the early spawners were larger than late spawners. The resulting progeny may reflect this adult condition.

Knowledge of pink salmon biology is limited, and little factual evidence can be presented as to the effects of physiological factors on size. Similarly, genetic studies of pink salmon have received little or no attention. The environmental factors, on the other hand, have been under intensive study and afford a basis of plausible factors which might produce size differences. In the light of present information, the author is inclined to credit early egg deposition, coupled with favorable thermal conditions, as the factor predominantly affecting size differences between early and late fry migrants.

I am indebted to Douglas G. Chapman of the University of Washington for statistical counsel.

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EXPERIMENTAL FARMING OF THE SOFT-SHELL CLAM, *MYA ARENARIA*, IN MASSACHUSETTS, 1949-1953

By Osgood R. Smith,* John P. Baptist,* and Edward Chin**

BACKGROUND

The clam-farming experiments which this paper describes were carried out over the years 1949-1953 on the tidal flats of Plum Island Sound, Essex County, Mass., and where noted, in the Hampton River, N. H. The commercially-important clam, *Mya arenaria*, had been becoming progressively scarcer along the coasts of Massachusetts, New Hampshire, and western Maine since about 1940, and it was generally believed that the scarcity was caused by overdigging. If overdigging was the principal cause, it was logical to assume from the work of Mead (1900-1904), Kellogg (1905), and Belding (1930) that clam farming would help to alleviate the shortage. Small clams could be taken from areas closed due to pollution and grown to market size in clean areas. Kellogg and Belding (op. cit.) had demonstrated that clams could be transplanted and that they would survive and grow well enough to produce an increase in volume, so our experiments were designed to learn more about methods and to find out if farming, either by towns or by individuals, would be feasible under present conditions.

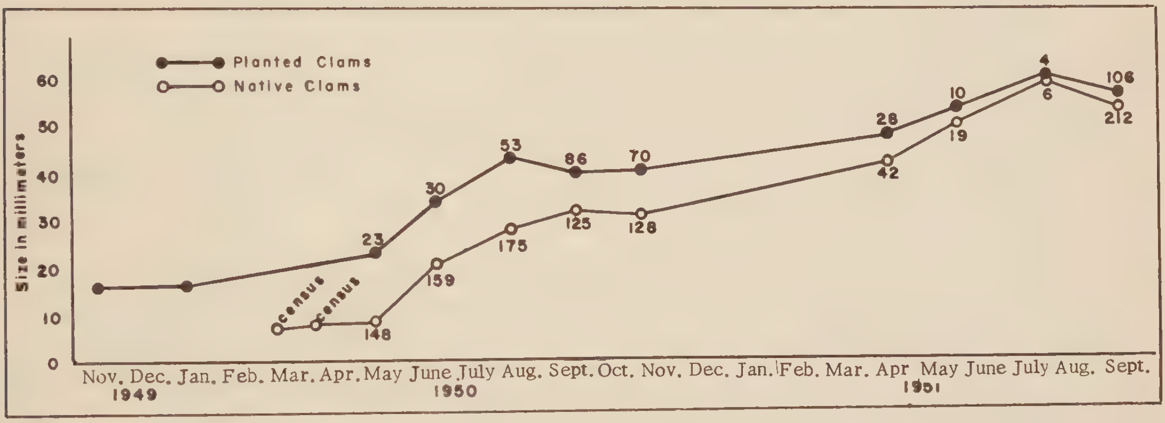

Fig. 1 - Growth of planted and native clams under chicken wire in plot 24B, based on average length from square-foot samples. Numbers of clams per square-foot sample are beside most datum points. Numbers beside points for September 1951 give numbers of clams in eight square feet. Datum point for planted clams in January is from plot 25. Points for native clams in March and April are from "open" flats around plot 24.

TRANSPLANTING METHODS

On May 26 and June 2, 1949, 16 bushels of clams averaging 39 mm. in length[1] were transplanted in Plum Island Sound at low tide (1) by broadcasting, (2) by plant-

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[1] Shell lengths were measured with vernier calipers to the nearest millimeter, and tabulated in two-millimeter groups, the odd number being combined with the next highest even number (Felin and Phillips 1948).

ing them in plowed furrows, (3) by broadcasting them on roughened ground at high tide, (4) by broadcasting from a boat. All these methods were commonly used by Massachusetts towns in 1949. The clams were planted in concentrations of about 20 and 38 per square foot.

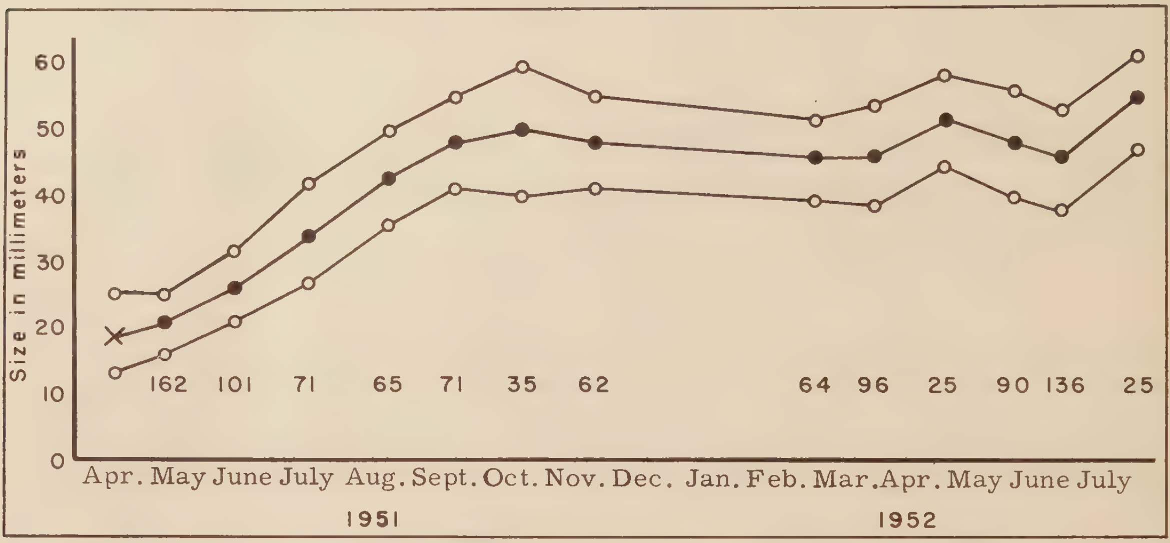

Fig. 2 - Solid points show average growth of planted clams in plots 45B and 60. Open circles above and below averages show one standard deviation. Numbers below datum points are numbers of clams in two square-foot samples from the two plots. The X at lower left is from a volumetric sample of clams just before they were planted.

Two quite different types of clam flats were tested: Hales Cove, a relatively soft flat, is composed of fine sand and silt, and Horseshoe Flat, a hard sandy flat with many shell fragments.

Examination and counts of clam holes in the various plots the day after transplanting indicated that broadcasting at low tide is fully as effective as any of the more laborious methods. This is in agreement with Belding (1930). Broadcasting from a boat may be even more effective for large areas, but in testing this method we were unable to keep the clams within the staked areas so we could not compare the results with other plots.

Within a week after the above plots had been set out, the horseshoe crab (*Limulus polyphemus*) had concentrated on them and dug up most of the clams. On June 7, 31 horseshoe crabs were found in three 10 x 20-foot plots on Horseshoe Flat, and the entire planted area was covered with depressions. On the softer soil of Hales Cove, the entire surface of the plots had been lowered enough to form square pools

Table 1 - Recoveries of Medium-Size Clams Transplanted August 17,1949, at Average Size of 33 mm. from Fenced Plot (#13)

Date Sampled	Area Sampled	Clams Recovered	Clams Per Sq. Ft.	Avg. Size	Avg. Growth
	Sq. Ft.	No.	No.	mm.	mm.
Aug. 22, 1949	2	52	26.0	-	0
Sept. 19, 1949	2	75	37.5	-	0
July 5, 1950	1	1	1.0	61	27
July 10, 1950	16	62	3.9	58	26
Aug. 30, 1950	16	92	5.8	63	32
Sept. 7, 1950	32	97	3.0	-	-
Oct. 20, 1950	3	19	6.3	62	26
Summary of all 1950 samples:	68	271	4.0	(Survival--about 12.5%)	

of water at low tide. When the Hales Cove plots were dug in November 1949, 92 percent of the clams had disappeared. Field observations and occasional trial digs indicated that most of the loss was caused by horseshoe crabs within a week after the clams were transplanted.

Green crabs (Carcinides maenas) probably dug some of the clams also, but we did not suspect their importance at that time. The principal result of this first series of transplanting experiments was to prove that natural predation was a major problem which would have to be met if clam farming was to be successful.

EXPERIMENTS ON METHODS OF COMBATTING NATURAL PREDATION

After the first transplanting experiments had been eliminated by predators, more plots were set out to test methods of keeping predators away from the clams by the use of fences and screens.

Table 2 - Recoveries of Large Clams Transplanted November 16, 1949, at Average Size of 46 mm. from Fenced and Unprotected Plots

Location	Plot No.	Estimated No. Planted Per Sq. Ft.	Recoveries				
			No. from 4-Sq.-Ft.	No. Per Sq. Ft.	Avg. Size in mm.	Avg. Size of "Planting Ann."	Date Sampled (1950)
Fenced Plots							
Hales Cove	14A	38	100	25.0	57	48	July 18
	15A	21	82	20.5	52	40	July 25
Horseshoe Flat	18A	38	182	45.5	57	44	July 21
	19A	21	85	21.3	55	43	
Summary:		118	449	28.1	(Survival 95%)		
Unprotected Plots							
Hales Cove	16A	38	94	27.0	58	50	July 18
	17A	21	36	9.0	56	41	July 25
Horseshoe Flat	21A	38	60	15.0	58	49	July 21
	20A	21	57	14.3	59	46	
Summary:		118	247	15.4	(Survival 52%)		

The first fenced plot (no. 13) was set out in August of 1949, following the then unpublished work of Turner (1949). This fence, and others built later, was made of 3-foot-wide poultry wire of 2-inch mesh. The lower edge was buried 6 inches, making a fence 2½-feet high. This fence kept out horseshoe crabs, so in November of 1949 two more series of plantings were set out on Horseshoe Flat and Hales Cove, arranged so that fences could be built around some of them the following spring. The clams were of 2 size groups--(1) the larger, dug commercially in Quincy, Mass., averaged 46.2 mm. in length, and (2) the smaller from Scarborough, Me., averaged 16.1 mm.

When these plots were set out, the horseshoe crabs had left the flats for the winter. Most of the green crabs had left and those that remained were nearly dormant. The only predators that seemed likely to attack the clams during the winter were ducks and gulls, because both of these had been seen "puddling" the flats with their feet to wash out small clams, as described by Medcof (1949). Therefore parts of several plots of small clams were covered with one-inch mesh chicken wire staked down flat on the soil soon after the clams had dug in.

Only one small piece of wire about 6 x 6 feet on plot no. 24B remained through the winter, but this one plot, as we shall see later, showed what clams may do where they are well protected.

Examination of tables 1, 2, and 3 will show the results from fenced and unprotected plots of large and small clams, and from a plot of small clams protected by chicken wire staked down over them. The effect of covering planted clams with chicken wire is further demonstrated by table 4, which shows results of transplanting experiments in 1951 and 1952. These will be discussed in detail later.

Table 3 - Recoveries of Small Clams Transplanted November 18, 1949, at Average Size of 16.1 mm. from Protected and Unprotected Plots

Location and Plot No.	Estimated No. Planted Per Sq. Ft.	Area Sampled (Sq. Ft.)	No. Per Sample	No. Per Sq. Ft.	Average Length in mm.	Average Length of Annulus Formed at Time of Planting	Date Sampled
Protected with Fence							
Hales Cove Plot 14B	216	1	7	7.0	54	22	Oct. 9, 1950
		1	4	4.0	54	21	
		1	7	7.0	54	21	
		5	9	1.8	57	24	Nov. 15, 1950
		7	22	3.1	58	22	
Summary:		15	49	3.3	(Survival--1.5%)		
Protected with Fence							
Hales Cove Plot 15B	108	1	1	1.0	45	18	Oct. 9, 1950
		1	2	2.0	50	20	
		1	1	1.0	57	23	
		16	11	0.7	54	21	Nov. 15, 1950
Summary:		19	15	0.8	(Survival--9.7%)		
Unprotected							
Hales Cove Plot 16B	216	1	0	0	-	-	Oct. 9, 1950
		1	0	0	-	-	
		1	0	0	-	-	
		6	0	0	-	-	Nov. 15, 1950
Unprotected							
Hales Cove Plot 17B	108	1	0	0	-	-	Oct. 9, 1950
		1	0	0	-	-	
		1	0	0	-	-	
		6	0	0	-	-	Nov. 15, 1950
Unprotected							
Hales Cove Plot 23	54	1	6	6	-	-	May 11, 1950
		1	3	3	-	-	June 22, 1950
		1	0	0	-	-	Aug. 9, 1950
		4	0	0	-	-	Nov. 1, 1950
Unprotected							
Hales Cove Plot 24A		1	10	10	-	-	May 11, 1950
		1	0	0	-	-	June 22, 1950
		1	0	0	-	-	Aug. 9, 1950
		1	0	0	-	-	Sept. 20, 1950
		1	0	0	-	-	Nov. 1, 1950
Protected with Chicken Wire for 2 Years							
Hales Cove Plot 24B	108	1	23	23	23.5	-	May 11, 1950
		1	30	30	34.2	-	June 22, 1950
		1	53	53	44.0	-	Aug. 9, 1950
		1	86	86	40.0	-	Sept. 20, 1950
		1	70	70	41.0	-	Nov. 1, 1950
		1	28	28	48.0	-	Apr. 12, 1951
		1	10	10	54.0	-	May 28, 1951
		1	4	4	61.0	-	July 26, 1951
		8	106	13	57.0	-	Sept. 11, 1951
Survival 12%--Sept. 11, 1951							
Protected by Wire Part of Winter, Clammers Dug in Plot							
Hales Cove Plot 25	108	1	20	20.0	16.7	-	Jan. 11, 1950
		1	5	5.0	14.2	-	
		1	30	30.0	24.8	-	May 19, 1950
		½	0	0	-	-	
		4	9	4.5	52.2	-	Sept. 18, 1950
		3	5	1.7	50.4	-	
Protected by Wire Part of Winter							
Horseshoe Flat Plot 26B	108	1	20	20.0	24.7	16.4	May 19, 1950
		1	1	1.0	37.0	19.0	July 5, 1950
Unprotected							
Horseshoe Flat Plot 26A	108	1	2	2.0	28.1	17.8	May 19, 1950
		1	0	0	-	-	July 5, 1950
Unprotected							
Horseshoe Flat Plot 27	108	1	15	15.0	24.9	16.2	May 19, 1950
		1	0	0	-	-	July 5, 1950

It should be explained that the fences kept out horseshoe crabs but not green crabs. By the summer of 1950 we had learned that green crabs, not birds, were digging up planted clams inside the fences. During the summer months we had watched the crabs going through and over the fences at high tide, and one crab was caught in the act of devouring a 50 mm. clam.

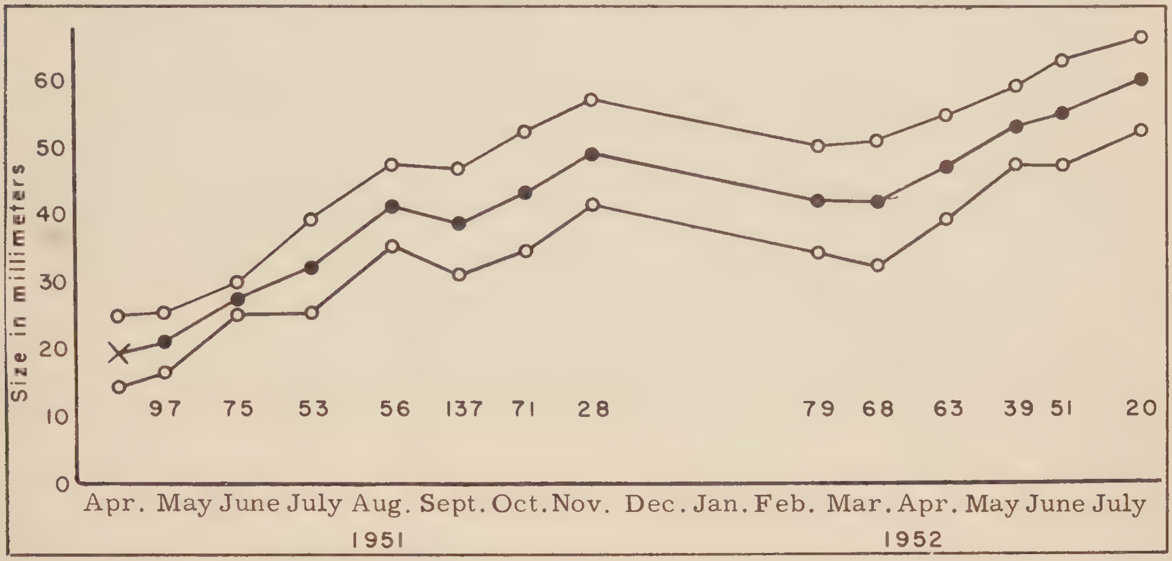

Fig. 3 - Solid points show average growth of planted clams in plot 46. Open circles above and below averages show one standard deviation. Numbers below datum points are numbers of clams in single square-foot samples. The X at lower left is from a volumetric sample of clams just before they were planted.

Table 4 - Recoveries from Protected and Unprotected Plots of Clams in Various Types of Soil (Planted April 17-19, 1951, at Average Length of 19 mm.)

Plot	Est. No. Planted Per Sq. Ft.	Plot Dim. (Ft.)	Number of Planted Clams Recovered in One-Square-Foot Samples														Protection
			1951							1952							
			May 10-11	June 12-13	July 16-17	Aug. 22-27	Sept. 20	Oct. 22	Nov. 23	March 3	March 31	May 1	June 3	June 25	July 30	
Hales Cove--Mod. Soft Fine Sand and Silt																	
45A	51	15x15	37	4	0	0	0	0								None
45B	51	15x15	51	50	16	48	54	33	13	51	57	38	26	40	11	Chicken wire
46	104	5x11	162	101	71	65	71	35	62	64	96	25	90	136	25	Chick. wire on frame
47	104	5x11	149	3	0	0	0	0								None
48	104	5x11	71	-	52	2	0		1	(Wire carried away in August)						Chicken wire
Ordway's--Firm Fine Sand and Silt																	
60A	51	15x15	42	1	1	0	0	0								None
60B	51	15x15	46	25	37	8	83	38	15	28	11	25	13	11	9	Chicken wire
Rowley "Finger Flat"--Loose Rippled Sand, Low																	
49A	51	15x15	9	0	0	0										None
49B	51	15x15	20	0	0	0	(Wire carried away early June)									Chicken wire
Thorofare--Hard Rippled Sand, High																	
51A	51	15x15	11	3	1	-	-	2								None
51B	51	15x15	13	3	9	-	-	7								Chicken wire
53A	104	10x10	39	0	0	-	-	3								None
53B	104	10x10	21	21	0	-	-	1								Chicken wire
Dole's Island Bar--Rippled Sand, Low																	
54	51	15x15	-	(Clams washed away when planted)												None
Dole's Island Pond--Soft Silt and Detritus, High																	
55	51	15x15	-	-	0	0	0									None
Jones Grant, Hampton River, N. H.--Mod. Soft Fine Sand and Silt																	
56A	25	15x30	-	-	2	Wire removed and most of clams dug up by clammers.									-	None
56B	25	15x30	-	-	13										-	Chicken wire
57A	51	15x15	-	-	4										0	None
57B	51	15x15	-	-	11										4	Chicken wire
59A	25	15x30	-	-	0										-	None
59B	25	15x30	-	-	(holes seen)										-	Chicken wire

Survival of the planted clams depended on both the size at planting and the degree of protection. Inside a fence, where green crabs could go but horseshoe crabs could not, about 95 percent of the large clams survived for 8 months. With no protection, only about 50 percent of the large clams survived for 8 months (table 2). There was little or no loss of large clams during the winter, but they became thinned out rapidly as soon as the horseshoe and green crabs became active in the spring.

No further work was done with large clams because those available were nearly market size (2 inches) when transplanted, and unless such clams were obtained by cheap mechanical means there would not be any profit in transplanting them.

The small (16 mm.) clams apparently were thinned out soon after planting, but thereafter survived the winter fairly well in all plots (table 3). Screened samples were not taken regularly enough to demonstrate this, but plot no. 25 was sampled in January and most of the other plots were examined in March and April 1950. The habit which small clams have of coming up out of the soil and moving about (Smith 1953) may account for some of the initial loss. Birds probably were responsible for some of the thinning, but the horseshoe crabs and green crabs were the predators that did the real damage. In March and April clams were still abundant enough in all sampled plots to produce good digging, but they were completely eliminated in most unprotected areas within a few weeks after the horseshoe and green crabs became active in the spring (see the May, June, and July samples in table 3). A few

Table 5 - Length Frequencies of Clams Transplanted November 18, 1949, from Plot 24B

Length in mm.	Sample of Planting Stock	Number of Clams Recovered in Square-Foot Samples									Clams from 8 Sq. Ft.
		1950						1951			
		Jan.[1] 11	May 11	June 22	Aug. 9	Sept. 20	Nov. 1	Apr. 12	May 28	July 26	Sept. 11
10	-	1	-	-	-	-	-	-	-	-	-
12	12	2	1	-	-	-	-	-	-	-	-
14	41	3	-	-	-	-	-	-	-	-	-
16	30	3	4	1	-	-	-	-	-	-	-
18	27	6	1	-	-	-	-	-	-	-	-
20	12	1	1	-	-	-	-	-	-	-	-
22	5	2	2	-	-	-	-	-	-	-	-
24	2	2	3	-	-	-	-	-	-	-	-
26	3	-	5	-	-	-	-	-	-	-	-
28	-	-	2	2	-	-	-	-	-	-	-
30	3	-	1	4	1	3	2	-	-	-	-
32	-	-	-	5	-	3	2	-	-	-	-
34	-	-	2	4	1	4	6	1	-	-	-
36	-	-	1	3	2	11	6	-	1	-	-
38	-	-	-	5	2	11	8	-	-	-	-
40	-	-	-	3	8	19	8	1	-	-	1
42	-	-	-	2	4	11	8	1	-	-	2
44	-	-	-	-	13	9	17	6	1	-	4
46	-	-	-	-	8	7	5	4	1	-	9
48	-	-	-	-	7	2	5	3	1	-	5
50	-	-	-	1	3	2	1	5	1	-	8
52	-	-	-	-	1	2	-	-	-	-	7
54	-	-	-	-	3	1	1	2	-	-	10
56	-	-	-	-	-	1	-	2	-	1	7
58	-	-	-	-	-	-	1	-	1	-	8
60	-	-	-	-	-	-	-	3	1	1	10
62	-	-	-	-	-	-	-	-	-	1	6
64	-	-	-	-	-	-	-	-	1	-	7
66	-	-	-	-	-	-	-	-	-	1	2
68	-	-	-	-	-	-	-	-	2	-	5
70	-	-	-	-	-	-	-	-	-	-	5
72	-	-	-	-	-	-	-	-	-	-	6
74	-	-	-	-	-	-	-	-	-	-	1
76	-	-	-	-	-	-	-	-	-	-	2
78	-	-	-	-	-	-	-	-	-	-	-
80	-	-	-	-	-	-	-	-	-	-	-
82	-	-	-	-	-	-	-	-	-	-	1
N	135	20	23	30	53	86	70	28	10	4	106
$\overline{X}$	16.1	16.7	23.5	34.2	43.5	40.1	40.7	48.3	53.9	60.7	56.9
Sx	3.65	3.12	6.08	5.99	4.78	5.19	5.37	5.63	10.25	3.59	16.79

[1] Sample from plot 25, adjacent to plot 24B which was not sampled at this time.

clams (0.7-1.5 percent) survived inside fences where they could be reached by green crabs but not by horseshoe crabs. So with small clams, the two predators under discussion are about equally bad; if one doesn't eat the clams the other will. Here again the effect of size may be seen. The survivors had annuli, formed at the time of planting, which indicate they were larger than the average for the lot when they were planted (see table 3). An intermediate situation in both size and percentage survival is shown by fenced plot no. 13 (table 1).

The one plot (no. 25) in which a few unprotected clams did survive was on firmly-packed fine sand and silt, near the bank of Plum Island. Unfortunately, clammers dug through this plot sometime during the first winter so we were unable to secure a reliable series of samples from it.

Table 6 - Length Frequencies of Clams Transplanted April 17, 1951, from Plot 45B

Length in mm.	Sample of Planting Stock	Number of Clams Recovered in Square-Foot Samples												
		1951							1952					
		May 10	June 12	July 16	Aug. 22	Sept. 20	Oct. 22	Nov. 23	March 3	March 31	May 1	June 3	June 25	July 30
10	-	-	-	-	-	-	-	-	-	-	-	-	-	-
12	34	-	-	-	-	-	-	-	-	-	-	-	-	-
14	103	2	-	-	-	-	-	-	-	-	-	-	-	-
16	151	3	1	-	-	-	-	-	-	-	-	-	-	-
18	152	10	4	-	-	-	-	-	-	-	-	-	-	-
20	115	14	1	-	-	-	-	-	-	-	-	-	-	-
22	83	14	7	1	-	-	-	-	-	-	-	-	-	-
24	53	2	10	-	-	-	-	-	-	-	-	-	-	-
26	25	2	10	-	1	1	-	-	-	1	-	-	-	-
28	22	-	7	1	-	1	-	-	1	2	-	-	-	-
30	19	2	3	2	-	1	1	-	4	2	-	-	-	-
32	8	-	2	5	2	2	1	-	3	5	1	-	-	-
34	4	1	1	2	4	3	-	-	1	5	1	-	-	-
36	5	1	2	1	5	6	2	-	-	2	1	-	1	-
38	3	-	1	3	5	8	4	2	7	3	1	-	1	-
40	3	-	-	-	6	3	2	-	10	7	4	1	-	-
42	2	-	-	-	5	5	1	1	4	4	4	1	-	-
44	-	-	-	-	5	2	3	-	2	1	3	-	2	-
46	1	-	-	-	9	3	2	-	3	8	4	4	2	2
48	2	-	1	1	3	5	2	3	4	6	4	2	3	-
50	-	-	-	-	-	4	3	-	4	5	2	4	3	1
52	-	-	-	-	1	5	3	1	2	2	2	2	5	-
54	-	-	-	-	-	1	5	1	2	-	2	1	2	2
56	-	-	-	-	2	2	-	1	2	2	2	2	6	-
58	-	-	-	-	-	2	1	1	-	-	2	2	5	2
60	-	-	-	-	-	-	2	2	-	2	1	1	4	-
62	-	-	-	-	-	-	-	-	1	-	-	2	2	1
64	-	-	-	-	-	-	-	-	1	-	2	3	3	-
66	-	-	-	-	-	-	1	1	-	-	2	-	1	1
68	-	-	-	-	-	-	-	-	-	-	-	1	-	2
70	-	-	-	-	-	-	-	-	-	-	-	-	-	-
N	785	51	50	16	48	54	33	13	51	57	38	26	40	11
$\bar{X}$	19.45	21	26	33.5	41.4	42.7	46.9	51.4	42.7	42.1	48.3	53.5	54.1	57.3
Sx	5.37	4.27	5.33	5.45	6.09	7.88	8.57	8.4	8.28	7.94	8.71	7.49	6.89	7.75

Expense seems to be the major obstacle to raising clams by protecting them with wire over the flats. These experiments were not on a large enough scale to give adequate production cost figures, but if we assume 1,200 legal clams per bushel (Turner 1950) and 20 clams per square foot, then 60 square feet of flat could produce a bushel. Wire to cover that area would cost around \$1.60, and it probably would have to be replaced once, bringing the cost for wire alone to around \$3 to \$4 a bushel.

Experiments in progress indicate that a small vertical fence with a flange on top may be a satisfactory means of protecting clams from horseshoe crabs and green crabs. According to Dr. P. Korringa of Holland,[2] the French oyster growers use a fence only 10 inches high (25 to 30 cm.) with a flange on top to protect oyster spat from green crabs. A barrier similar to this was tried in Plum Island Sound in the summer of 1952. This fence acted as a partial barrier, but it was too small and was eroded badly, so results were not conclusive. A much larger and stronger fence was built in 1953. This fence was built in the shape of a circle, to enclose the largest possible area per unit length and avoid eddy-producing corners. It was 300 feet in circumference, 18 inches high, and the flange was made of 1- by 6-inch boards, each 10 feet long. The boards were lapped instead of butted to simplify construction. The stakes were 2 by 2 inches; a 4-foot stake was driven in the mud at each overlap of the boards and a 3-foot stake driven in between. One-inch mesh chicken wire, 2 feet wide, was stapled on the inside of this wooden structure, and the bottom edge buried about 6 inches. The actual construction took about 15 man-hours, or 3 men one tide and 2 men the next. The fence proved to be very rigid, and probably stronger than necessary.

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[2] Unpublished letter from Dr. P. Korringa of the Ruksinstituut voor Visscherijonderzoek Bergen op Zoom, Holland, to John Glude, Chief, Clam Investigations, U. S. Fish and Wildlife Service, Boothbay Harbor, Me.

Table 7 - Length Frequencies of Clams Transplanted April 17, 1951, from Plot 46

Length in mm.	Sample of Planting Stock	Number of Clams Recovered in Square-Foot Samples												
		1951							1952					
		May 10	June 13	July 16	Aug. 22	Sept. 20	Oct. 22	Nov. 23	March 3	March 31	May 1	June 3	June 25	July 30
10	-	-	-	-	-	-	-	-	-	-	-	-	-	-
12	34	-	-	-	-	-	-	-	-	-	-	-	-	-
14	103	7	-	-	-	-	-	-	-	-	-	-	-	-
16	151	25	1	-	-	-	-	-	-	-	-	-	-	-
18	152	43	7	-	-	-	-	-	-	-	-	-	-	-
20	115	27	4	1	-	-	-	-	-	-	-	-	-	-
22	83	28	20	1	-	-	-	-	-	-	-	-	-	-
24	53	9	26	2	-	-	-	-	-	-	-	-	-	-
26	25	6	9	8	-	-	-	-	-	-	-	-	1	-
28	22	5	9	9	1	-	1	-	-	-	-	1	-	-
30	19	5	6	11	-	-	-	-	-	2	-	-	-	-
32	8	4	7	4	2	1	-	-	-	4	-	-	1	-
34	4	1	4	11	5	-	-	1	3	1	-	4	-	-
36	5	1	3	3	6	2	2	1	4	5	-	6	7	-
38	3	-	3	3	6	1	1	2	2	8	1	2	12	-
40	3	1	1	1	7	6	4	1	7	6	-	4	12	-
42	2	-	-	6	8	5	1	4	5	5	2	9	16	-
44	-	-	1	4	9	9	2	5	8	6	3	8	19	1
46	1	-	-	1	5	13	-	10	7	16	2	5	11	2
48	2	-	-	1	3	9	1	11	9	10	-	9	11	3
50	-	-	-	3	7	8	5	8	7	10	2	11	13	5
52	-	-	-	2	-	-	5	8	4	5	3	5	10	1
54	-	-	-	-	2	5	3	2	3	9	4	9	9	2
56	-	-	-	-	3	5	2	2	3	1	2	6	4	4
58	-	-	-	-	1	-	2	4	2	5	2	2	2	2
60	-	-	-	-	-	3	2	1	-	1	2	2	2	-
62	-	-	-	-	-	1	1	2	-	1	1	5	4	3
64	-	-	-	-	-	3	-	-	-	-	-	-	-	-
66	-	-	-	-	-	-	1	-	-	-	1	1	-	1
68	-	-	-	-	-	-	1	-	-	1	-	1	1	-
70	-	-	-	-	-	-	-	-	-	-	-	-	-	-
72	-	-	-	-	-	-	1	-	-	-	-	-	1	-
74	-	-	-	-	-	-	-	-	-	-	-	-	-	1
76	-	-	-	-	-	-	-	-	-	-	-	-	-	-
78	-	-	-	-	-	-	-	-	-	-	-	-	-	-
N	785	162	101	71	65	71	35	62	64	96	25	90	136	25
$\bar{X}$	19.45	20.5	25.9	34.1	42.7	47.9	50.4	48.3	45.6	46.0	51.7	48.0	46.3	54.2
Sx	5.37	4.65	5.46	7.71	7.02	6.88	9.60	7.14	6.15	7.56	6.96	8.16	7.34	6.90

During the summer of 1953 this fence effectively protected clams from the horseshoe and green crabs, their two worst enemies. Figure 5 shows the flat outside the fence has been completely dug up while the surface inside is still smooth. A baited green-crab trap set inside the fence caught 24 crabs in 24 hours, but only 3 of these were too large to have gone through the meshes of the chicken wire fence. A similar trap outside the fence caught 111 green crabs, and, as is usual in trap samples, very few of the crabs were small. The effectiveness of the fence was also observed by swimming around it with an "Aqualung" at high tide, when the water was about 7 feet deep. Large and medium green crabs were clustered against the fence all around its circumference, averaging about 1 every 2 feet of fence. Some were at the base, some were clinging to the wire, but fully half were clinging to the wire up under the flange. Several small crabs and one large one were found inside. The small ones could have gone through the meshes, or they might have swum over the fence because one was seen in the act of swimming over it. While observing these crabs, it became quite obvious that little ones swim much more than big ones.

No horseshoe crabs were ever found inside the fence. Those seen around the fence usually went off in some other direction after bumping into the wire, apparently no effort being made to get over or under the fence.

Apparently the small crabs that went through and over the fence were not numerous or large enough to do serious damage to the clam crop.

Table 8 - Length Frequencies of Clams Transplanted April 19, 1951, from Plot 60B

Length in mm.	Sample of Planting Stock	Number of Clams Recovered in Square-Foot Samples												
		1951							1952					
		May 11	June 12	July 17	Aug. 27	Sept. 20	Oct. 23	Nov. 26	March 3	March 31	May 1	June 3	June 25	July 30
10	-	-	-	-	-	-	-	-	-	-	-	-	-	-
12	34	-	-	-	-	-	-	-	-	-	-	-	-	-
14	103	3	-	-	-	-	-	-	-	-	-	-	-	-
16	151	5	-	-	-	-	-	-	-	-	-	-	-	-
18	152	10	-	-	-	-	-	-	-	-	-	-	-	-
20	115	6	2	3	-	-	-	-	-	-	-	-	-	-
22	83	7	4	2	-	-	-	-	-	-	-	-	-	-
24	53	8	6	1	-	4	-	-	-	-	-	-	-	-
26	25	2	1	4	-	3	1	-	-	-	-	-	-	-
28	22	1	6	5	-	2	2	-	1	-	-	-	-	-
30	19	4	2	1	-	12	2	-	2	1	-	-	-	-
32	8	-	1	7	-	8	4	-	-	1	-	-	-	-
34	4	-	-	3	1	11	4	1	3	-	1	-	-	-
36	5	-	-	4	-	8	3	1	2	-	1	-	-	-
38	3	-	1	1	1	7	4	1	2	1	2	-	-	-
40	3	-	1	2	2	6	4	-	3	1	3	-	-	-
42	2	-	-	2	1	8	2	1	2	-	-	-	-	-
44	-	-	1	-	1	3	1	-	3	1	3	1	1	-
46	1	-	-	1	-	4	4	2	2	3	4	2	-	-
48	1	-	-	1	-	2	4	1	2	2	5	3	-	-
50	-	-	-	-	2	1	3	3	2	1	3	3	-	-
52	-	-	-	-	-	1	-	-	3	-	-	-	1	1
54	-	-	-	-	-	2	-	2	-	-	2	2	-	-
56	-	-	-	-	-	1	-	2	1	-	-	-	1	-
58	-	-	-	-	-	-	-	-	-	-	1	-	2	1
60	-	-	-	-	-	-	-	-	-	-	-	2	-	-
62	-	-	-	-	-	-	-	1	-	-	-	-	2	2
64	-	-	-	-	-	-	-	-	-	-	-	-	1	1
66	-	-	-	-	-	-	-	-	-	-	-	-	-	2
68	-	-	-	-	-	-	-	-	-	-	-	-	2	-
70	-	-	-	-	-	-	-	-	-	-	-	-	-	1
72	-	-	-	-	-	-	-	-	-	-	-	-	1	1
74	-	-	-	-	-	-	-	-	-	-	-	-	-	-
N	785	46	25	37	8	83	38	15	28	11	25	13	11	9
$\overline{X}$	19.45	21.0	27.2	32.2	42.3	36.5	38.9	48.1	41.9	42.5	45.5	50.6	60.6	63.7
Sx	5.37	4.36	5.93	5.04	5.24	7.27	6.99	7.73	7.39	6.42	5.75	4.91	7.95	6.15

The fence was not standing long enough to tell just what effect it would have on the native clams, but it protected a small plot of transplanted clams. On July 28, 1953, about a bushel of clams averaging 17 mm. in length were planted, some inside and some outside the fence. Those outside never had a chance. With a face plate we could see green crabs grabbing many of them, and apparently none of them survived more than a few days. Inside the fence the clams dug in well, and a small plot within the fence was well peppered with their holes all summer. A square-foot sample on October 14 had 53 per square feet averaging 24 mm.

We planned to maintain this fence at least one more summer, to learn more about what could be produced by protecting a natural set, but clam diggers dug over the area early in 1954 so that particular fenced plot was abandoned.

Instead of rebuilding the fence, we worked with the towns of Ipswich, Mass., and Hampton, N. H., in helping them build fences similar to ours. Both towns purchased materials and supplied much of the labor. Unfortunately, neither of these fences was successful. The one at Ipswich clogged badly with seaweeds and colonial hydroids and could not be maintained. The one at Hampton stayed up well but it did not save either native or transplanted clams inside. Crab traps set inside and outside the Hampton fence indicated the damage was done by large numbers of crabs just small enough to go through the one-inch mesh. Crab traps fished 24 hours inside the fence on July 29, 30, and August 12, took 203, 89, and 93 crabs, respectively. The average widths were 40, 40, and 41 mm. Ninety-one percent of these were under 45 mm. wide, and therefore small enough to get through the meshes of the chicken wire. Control samples outside collected 266, 128, and 176, and the average widths were 47, 48, and 49 mm.

In view of these experiences, further fencing experiments will be done with finer-mesh wire. This should be effective if it can be maintained without clogging or washing too badly.

ATTEMPTS TO PLANT CLAMS SO AS TO AVOID PREDATORS

In April of 1951 another series of plots was set out in Plum Island Sound and in the Hampton River, N. H., to test survival on various types of flats and to get more reliable growth and survival data.

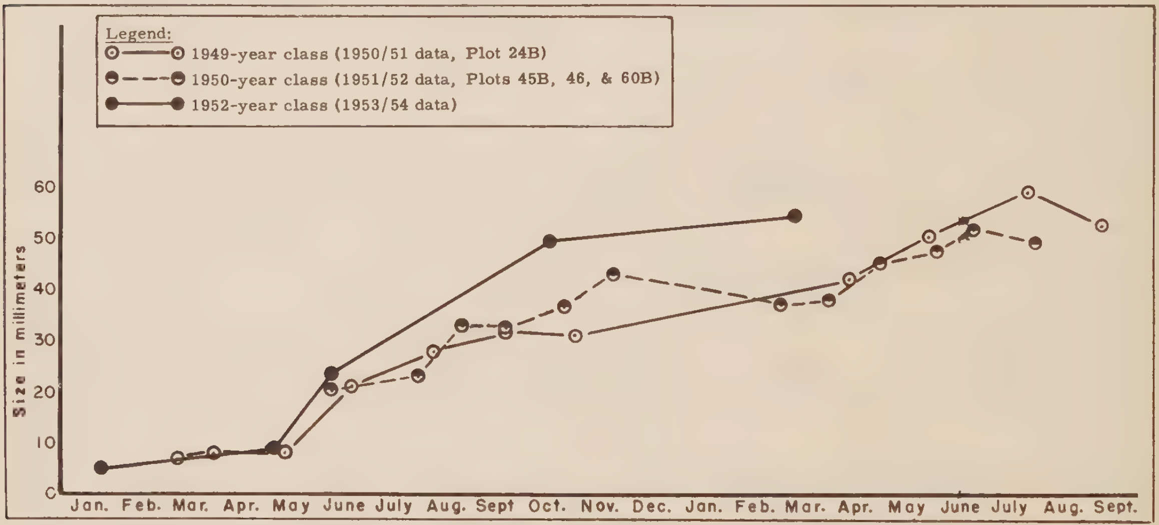

Fig. 4 - Comparative growth of native clams of 1949, 1950, and 1952 year-classes. Data for 1949 and 1950 are from protected plots, there being almost no survival elsewhere. Data for 1952 year-class are from unprotected areas, where clams survived and produced commercial digging, possibly because of more rapid growth.

This plan was adopted because the uneven distribution of native clams in Plum Island Sound, and the results from plot no. 25 mentioned above led us to believe that some areas might be more free of predators than others. Catches of green crabs in traps also indicated that high sandy flats had fewer crabs on them than muddy flats.

The results from these plots of transplanted clams are summarized in Table 4. It may be seen that the results at Hales Cove and Ordways confirmed the results of plot no. 24B (table 3) in showing that clams in those flats survived only where protected.

On the more sandy flats results were confused by the fact that the covering wire was carried away, undermined at the edges, or buried by 3 to 6 inches of shifting sand. Judging by the May samples, many of the clams washed away before they could establish themselves. On one high sandy bar, "Thorofare," the clams that did get established survived longer than in the muddy flats, but survival was not high enough in any unprotected plot to give profitable results.

SURVIVAL OF PROTECTED PLANTED CLAMS

In protected plot 24B, we established the planting density at 108 clams per square foot, and the recovery 2 years later, on a basis of 8 square feet, was 13 clams per square foot or about 12 percent.

In the protected plots 45B, 46, and 60B, survival was estimated from the average of the last four samples and the known concentration when planted. Plots 45B and 60B were each planted with 50 clams per square foot, and the average survival for the two plots combined (i.e., 8 square-foot samples) was 43 percent. Plot 46 planted with 100 per square foot apparently had a 69-percent survival, but the samples from that plot were quite variable. In any case, the clams were extremely crowded over the entire plot, probably too crowded for good growth, so we know survival was relatively high. Plot 46 not only was planted more densely than the others but it also was much better protected. It was covered by chicken wire on a frame, supported 1 inch above the surface of the soil by boards set edgewise in the mud. A few Polinices heros were found under this wire, but it kept green crabs and horseshoe crabs out better than wire that was just staked down. Crabs were sometimes found under the edges of the wire that was staked down.

Table 9 - Length Frequencies of Native Clams from Plot 24B, Chicken Wire-Protected from November 18, 1949 (History of 1949 Year-Class Shown by Figures below the Heavy Lines)

Length in mm.	Number of Clams Recovered in Square-Foot Samples									Clams from[4] 8 Sq. Ft. Sept. 11, 1951
	1950					1951				
	May 11	June 22	Aug. 9	Sept.[1] 20	Nov. 1	April 12	May 28	July[2] 26	Sept.[3] 11	
2	-	-	1	105	149	77	5	6	11	-
4	26	3	30	74	275	457	226	17	89	-
6	31	11	33	48	35	215	164	1	7	-
8	34	26	20	39	16	94	67	1	5	-
10	26	24	32	12	4	30	20	1	-	-
12	17	7	13	18	3	23	7	-	-	-
14	6	9	1	10	1	7	2	-	-	-
16	3	14	1	6	1	5	3	-	-	-
18	4	29	1	1	-	-	7	-	-	-
20	-	23	2	-	3	-	1	-	-	-
22	-	34	3	3	6	-	4	-	-	-
24	-	17	16	7	4	-	-	-	-	-
26	1	12	21	12	20	-	-	-	-	-
28	-	5	31	13	23	1	1	-	-	-
30	-	5	27	19	12	5	-	-	-	-
32	-	3	31	10	18	-	-	-	-	6
34	-	1	14	19	11	6	1	-	-	1
36	-	-	13	28	8	2	1	-	-	1
38	-	-	7	6	11	3	-	-	-	6
40	-	-	5	6	6	2	1	-	-	6
42	-	-	2	-	3	4	1	1	-	8
44	-	-	-	1	1	7	2	-	-	16
46	-	-	-	1	-	2	1	-	-	7
48	-	-	-	-	1	-	1	1	-	18
50	-	-	-	-	-	1	1	-	4	19
52	-	-	-	-	-	1	-	-	1	13
54	-	-	-	-	-	4	-	-	1	15
56	-	-	-	-	-	1	2	-	3	19
58	-	-	-	-	-	2	3	-	1	14
60	-	-	-	-	-	1	-	-	3	16
62	-	-	-	-	-	-	1	-	2	12
64	-	-	-	-	-	-	-	1	1	12
68	-	-	-	-	-	-	1	1	2	7
70	-	-	-	-	-	-	-	-	-	2
72	-	-	-	-	-	-	-	-	-	1
74	-	-	-	-	-	-	-	-	-	3
76	-	-	-	-	-	-	-	-	-	2
78	-	-	-	-	-	-	-	-	-	-
80	-	-	-	-	-	-	-	-	-	-
82	-	-	-	-	-	-	-	-	-	1
N	148	223	304	438	611	950	525	32	130	212
	Following data from clams below solid line only (growing part of 1949 year-class):									
N	148	159	175	126	127	42	19	6	-	212
$\overline{X}$	8.48	20.77	28.08	31.98	31.04	42.04	50.6	59.33	-	53.51
Sx	3.70	4.60	9.26	4.95	4.80	8.48	11.47	10.39	-	9.64

[1] Thirty-two mesh sampler used.
[2] Sample probably partly in area previously dug.
[3] This is only one of eight square-foot samples taken with fine-mesh screen.
[4] Large clams only, including those in previous column.

We do not know what happened to most of the clams that did not survive. Empty shells were found, but not enough to account for all the loss.

Survival was high enough in all protected plots to produce good commercial clam digging. Plot 24B produced about 25 legal clams per square foot, including natives; plot 45B produced about 16; plot 46, 23; plot 60B, about 9. Legal-size native clams were practically absent from the last 3 plots. These figures include only clams over 50 mm., and it may be seen by tables 5 to 10 that many smaller clams were "coming along," so final production would be somewhat greater.

GROWTH OF PLANTED AND NATIVE CLAMS

Transplanted clams usually were distinguishable from natives because their shells were characteristic of the region from which they had come. The clams from Scarborough, Maine, had rather chalky-appearing shells and they tended to be more round than Plum Island Sound clams. The ones from Quincy, Mass., usually had thick and deformed shells. The shells of native Plum Island Sound clams were generally smooth, slightly glossy, and more pointed posteriorly than either Scarborough or Quincy shells. The new shell, put on as the clams grew after transplanting, was typical of Plum Island Sound shells, and therefore the size at planting or the "planting annulus" could be identified and measured. A few individual clams were difficult to identify, but with these we consulted each other and arrived at a consensus. Annular rings, which form on clam shells much as they do on fish scales,

Table 10 - Combined Length Frequencies of Native Clams from Three Plots (45B, 46, and 60B), Protected (History of 1950 Year-Class is Shown by Figures Below the Solid Lines)

Length in mm.	Number of Clams Recovered in Three Square-Foot Samples												
	1951							1952					
	May 10-11	June 12	July 16-17	Aug. 22-27	Sept. 20	Oct. 22-23	Nov. 23-26	March 3	March 31	May 1	June 3-5	June 25-26	July 30 Aug. 1
2	13	4	5	100	251	146	100	19	28	43	21	-	26
4	295	181	94	339	841	935	435	64	70	524	170	4	122
6	249	93	54	53	27	78	99	33	17	327	74	6	11
8	88	40	15	13	10	7	19	29	27	128	39	8	2
10	48	11	9	4	4	1	-	28	29	58	12	5	1
12	32	-	2	-	3	-	-	16	36	20	8	1	-
14	17	2	1	-	-	1	1	2	10	11	4	3	-
16	8	5	2	-	1	-	-	1	1	20	9	2	-
18	1	8	3	1	1	-	-	2	1	9	3	3	-
20	2	5	6	-	-	-	-	1	-	7	4	2	1
22	3	2	5	2	1	-	-	-	-	-	10	5	-
24	-	-	2	1	2	1	-	-	1	1	6	4	-
26	-	5	1	1	3	2	-	-	-	-	2	6	1
28	-	2	2	-	4	-	1	2	2	-	-	4	1
30	-	1	1	1	2	-	-	1	3	-	1	11	2
32	-	-	1	3	4	2	1	2	3	-	-	4	1
34	-	-	1	-	2	1	-	4	4	-	1	1	1
36	-	-	1	-	6	1	1	2	6	1	1	-	1
38	-	-	1	2	4	2	1	5	3	-	-	1	-
40	-	-	-	4	-	1	1	3	1	-	2	-	2
42	-	-	-	2	2	1	1	5	6	2	1	1	1
44	-	-	-	1	-	-	2	-	2	-	-	1	1
46	-	-	-	-	-	-	2	-	3	1	-	2	-
48	-	-	-	-	-	-	3	-	2	-	2	1	-
50	-	-	-	-	-	1	-	-	2	3	-	-	2
52	-	-	-	-	1	-	1	-	-	-	1	2	2
54	-	-	-	-	-	-	1	-	-	-	-	-	1
56	-	-	-	-	1	-	-	1	-	-	2	2	-
58	-	-	-	-	-	-	-	-	-	-	1	1	-
60	-	-	-	-	-	1	-	-	-	-	-	1	-
62	-	-	-	-	-	-	-	-	-	-	1	1	-
64	-	-	-	-	-	-	-	-	-	-	-	-	-
66	-	-	-	-	-	-	-	-	-	-	-	-	1
68	-	-	-	-	-	-	-	-	-	-	-	-	-
70	-	-	-	-	-	-	-	-	-	-	-	1	-
	Following data from clams below solid line[1] only (growing part of 1950 year-class):												
N	-	30	27	18	34	13	15	25	38	7	12	14	10
$\bar{X}$	-	20.4	23.3	33.4	32.6	36.8	43.1	37.4	38.1	45.1	47.7	52.1	49.0
Sx	-	3.24	6.14	7.95	8.20	9.66	7.00	5.70	6.57	5.02	8.89	6.23	7.54

[1] The sample taken in May was not used for average size of the growing group because of the rather extreme dominance of 4 and 6 mm. clams which do not appear to grow.

were not as distinct as the rings formed when the clams were transplanted. Growth was determined from average sizes (lengths) of clams sampled at various times.

In plot 24B clams planted at 16 mm. in November 1949 reached an average size of 57 mm. at the end of the two following summers (fig. 1).

In plots 45B, 46, and 60B clams planted in April 1951 at 19 mm. grew to averages of 54, 57, and 63 mm., respectively, in two summers. Data from plots 45B and 60B have been combined to lessen variability because both were planted at a density of about 50 per square foot and subsequent treatment was the same. Plot 46 was planted with 100 clams per square foot and, as mentioned above, it was better protected (figs. 2 and 3).

Table 11 - Length Frequencies of Native Clams from Hales Cove (History of the 1952 Year-Class is Shown by Figures Below the Solid Lines)

	Number of Clams Recovered from Samples												
	1952								1953				1954
	July 12	July 30	Aug. 15	Aug. 28	Sept. 16	Sept. 29	Oct. 13	Oct. 28	Jan. 26	May 8	June 9	Oct. 14-20	March 11
No. Sq. Ft.	1	1	1	1	1	1	1	1	3	2	4	5-6[1]	2-20[2]
Length in mm.													
2	1	4	5	180	63	86	154	38	6	2	3	297	-
4	3	26	24	305	275	306	444	124	30	34	14	706	17
6	-	1	3	10	10	2	10	-	17	28	3	94	16
8	-	-	-	-	1	-	-	-	7	33	-	18	7
10	-	-	-	-	-	-	-	-	1	18	-	6	4
12	-	-	-	-	-	-	-	-	1	11	1	3	4
14	-	-	-	-	-	-	-	-	1	13	1	5	4
16	-	-	-	-	-	-	-	-	-	5	2	1	-
18	-	-	-	-	-	-	-	-	-	15	3	-	-
20	-	-	-	-	-	-	-	-	-	3	4	2	-
22	-	-	-	-	-	-	-	-	-	1	3	-	-
24	-	-	-	-	-	-	-	-	-	-	4	-	2
26	-	-	-	-	-	-	-	-	-	-	6	-	-
28	-	-	-	-	-	-	-	-	-	-	9	-	-
30	-	-	-	-	-	-	-	-	-	-	1	-	-
32	-	-	-	-	-	-	-	-	-	-	1	-	-
34	-	-	-	-	-	-	-	-	-	-	1	1	-
36	-	-	-	-	-	-	-	-	-	-	-	-	-
38	-	-	-	-	-	-	-	-	-	-	-	-	-
40	-	-	-	-	-	-	-	-	-	-	-	2	4
42	-	-	-	-	-	-	-	-	-	-	-	7	3
44	-	-	-	-	-	-	-	-	-	-	-	5	8
46	-	-	-	-	-	-	-	-	-	-	-	16	16
48	-	-	-	-	-	-	-	-	-	-	-	6	15
50	-	-	-	-	-	-	-	-	-	-	-	13	22
52	-	-	-	-	-	-	-	-	-	-	-	10	28
54	-	-	-	-	-	-	-	-	-	-	-	6	28
56	-	-	-	-	-	-	-	-	-	-	-	3	20
58	-	-	-	-	-	-	-	-	-	-	-	5	22
60	-	-	-	-	-	-	-	-	-	-	-	1	14
62	-	-	-	-	-	-	-	-	-	-	-	1	5
64	-	-	-	-	-	-	-	-	-	-	-	1	6
66	-	-	-	-	-	-	-	-	-	-	-	1	3
68	-	-	-	-	-	-	-	-	-	-	-	-	1
70	-	-	-	-	-	-	-	-	-	-	-	-	-
72	-	-	-	-	-	-	-	-	-	-	-	-	2
74	-	-	-	-	-	-	-	-	-	-	-	-	-
76	-	-	-	-	-	-	-	-	-	-	-	-	2
78	-	-	-	-	-	-	-	-	-	-	-	-	1
80	-	-	-	-	-	-	-	-	-	-	-	-	1
	Following data from clams below solid line only (growing part of 1952 year-class):												
N	4	31	32	495	349	394	608	162	63	163	36	78	201
$\bar{X}$	3.5	3.8	3.87	3.31	3.7	3.57	3.85	3.53	5.1	9.3	23.8	49.4	53.8
Sx	4.99	1.39	1.01	1.04	0.9	0.8	0.93	0.8	7.38	4.74	3.99	6.33	7.15

1/ Six square feet sampled, fine mesh (16) used on only 5 square feet.

2/ Two square feet screened with 12-mesh screens. Clams over 24 mm. dug from about 20 square feet.

It may be seen that all growth curves for planted clams show rapid growth in the spring and early summer, and little or no growth in fall and winter. There appears to be a shrinkage of the shell during the winter. This may actually occur, due to erosion or chipping of the edge of the shell, as suggested by Swan (1952). However, we have found that sizes of clams are inversely correlated with the number of clams per sample and it also happens that most of the points showing departures from a smooth growth curve are similarly associated with either unusually large or unusually small samples (see figs. 1, 2, and 3).

The effect of varying degrees of crowding within one small plot was shown by the 8 separate square-foot samples from plot 24B taken September 11, 1951, as well as by the departures from a smooth growth curve. Clams in the more crowded parts of the plot were distinctly smaller in average size. A correlation between average size and total number of native and planted clams gave a correlation coefficient of -0.8. The differences in size appear to be due to some sort of space relationship rather than lack of food; inasmuch as the square-foot samples adjoined, the entire plot was only 6 x 6 feet, and there were almost no clams in the surrounding flat to remove food from the water flowing over them. The above mentioned samples were as follows:

Number of Clams per square foot	- 18	22	23	25	26	32	72	100
Average size of Clams in mm.	- 60	55	64	58	60	59	50	51

The chicken wire put down to protect transplanted clams naturally gave some protection to natives. Small clams were sampled by screening the top 3 or 4 inches through 16 x 14 per-inch-mesh screening and the lower soil through 4-per-inch-mesh screening. The largest clams were usually picked by hand.

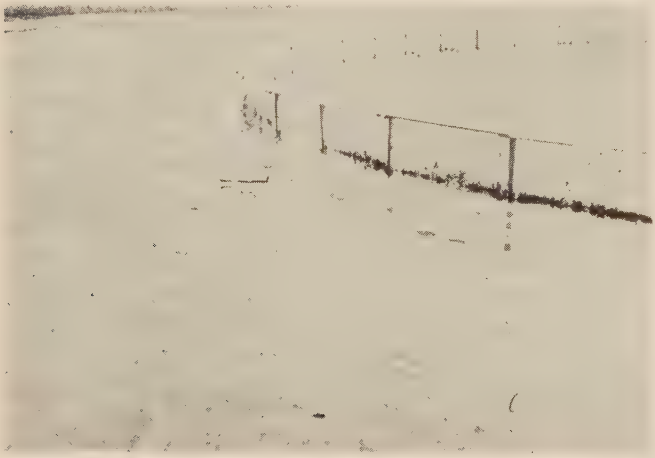

Fig. 5 - Fence built in Plum Island Sound, Newbury, Mass., June 3, 1953, to protect clams from horseshoe and green crabs. The photograph was taken about three weeks after the fence was built. Note that entire flat outside fence is covered with excavations of predators, while the soil inside is still smooth.

The growth of native clams was determined by comparing average lengths of the growing portion of a year class in successive samples. The small clams appearing in the May and June samples were considered to be from the previous summer's spawning because very few clams spawn earlier than May or June (Coe & Turner 1938), and also because the size frequencies of small clams sampled in late fall, winter, and early spring indicate that the May and June crop could belong to the year-class that had been spawned the previous summer. By May these clams are noticeably larger than they were in January, and by June most of the size frequencies are distinctly bi-modal. Of the two groups, the one containing the larger clams is what we have called the "growing portion," because its growth can be traced over at least two years, while the group of smaller clams does not seem to grow. Actually, the apparent lack of growth could be due to movement of the byssus-bearing clams, recruitment, or some change in the predator-prey relationships. Horseshoe crabs and green crabs, becoming active in the spring, might tend to concentrate on clams around 10 to 14 mm. which, if true, could cause the "trough" in the length-frequency curve.

During the summer of 1950 the natives in the only covered plot, no. 24B (table 9 and fig. 1), survived and grew so well that by September of 1951 there was an average of about 16 legal-size natives per square foot. These were clams of the 1949 year-class. Thus, the growth from plankton stage to market size took only three summers, or perhaps a little over two years.

In the three successful plots set out in the spring of 1951, small native clams were present at all times, but comparatively few survived and grew. We do not know why identical treatment produced a good crop one year and very little the next, when there were as many or more young clams. However, by adding the size-frequency data for native clams from these three plots, as in table 10, a growth curve may be derived for the protected natives of the 1950 year-class. Their growth is similar to that of the 1949 year-class (see fig. 4).

In the unprotected plots and the surrounding natural tidal flats, there was practically no survival from the 1949 or 1950 year-class. No data were secured for growth of the 1951 year-class, because no screens were down to protect it, and as with the 1949 and 1950 year-classes, there was practically no survival in the natural flats. There was practically no digging in the area, and none in our plots, so the failure of these crops was not caused by overdigging.

In marked contrast with the foregoing classes, the 1952 year-class survived well enough, even without protection, to produce some reasonably good commercial digging in upper Plum Island Sound. This year-class was not sampled as often nor as thoroughly as the others, but no sampling was needed to recognize its success during the summer of 1953. For the first time in four years the flats became pitted with clam holes, and from 8 to 15 diggers have been working on the Newbury flats almost every day from the fall of 1953 to the fall of 1954. The concentrations varied from 3 or 4 legal-size clams per square foot to about 20 from midsummer on.

The success of the 1952-class seems to have been due to rapid growth. See tables 9, 10, and 11, and figure 4 for a comparison of the 1952 year-class with the 1949 and 1950 year-classes. The larger size of this year-class of clams enabled them to dig deeper and thus be less accessible to predators. The small byssus clams, 12-15 mm. and under, were not unusually abundant during the winter of 1952/53, and as far as we could determine, predators were as abundant as ever. Therefore, we have no evidence that the success of the 1952 clams was due to any changes in the numerical relationships between predators and prey.

CONCLUSIONS

Natural predation on clams up to at least 50 mm. long is a serious problem which will have to be met if clam farming or transplanting is to be economically feasible. Horseshoe crabs and green crabs are the two most serious predators in New Hampshire and northern Massachusetts. Clams can be protected from these predators by covering flats with one-inch mesh chicken wire. In this way both native and transplanted clams can be grown from around 10 or 20 mm. to the market size of 2 inches, or about 50 mm. in two summers. Native clams under about 10 mm. long may or may not survive and grow under the chicken wire. The principal disadvantage of putting chicken wire over the clams is the expense of the wire, which might come to $3 or $4 per bushel of clams. Fences only 10-12 inches high with a flange on top may afford adequate protection and be cheaper per acre, but further experiments are required to demonstrate their successful practical application.

Growth of native clams in areas studied is rapid, from plankton stage to market size generally taking only three summers or perhaps a little over two years. One year-class (1952) grew even faster, producing a commercially-diggable crop in two summers, or a little over one year. This was the first year-class in at least 4 years to survive well enough, without protection, to produce good commercial digging. The success of this year-class and the failure of others, that were just as abundant up through the byssus stage, indicates that fluctuations in clam populations are largely natural in origin and may result from things other than fluctuations in the numbers of juvenile or byssus-stage clams.

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THE EFFECT OF SOME SULFONAMIDES ON THE GROWTH OF BROOK TROUT, BROWN TROUT, AND RAINBOW TROUT

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THE EFFECT OF SOME SULFONAMIDES ON THE GROWTH OF BROOK TROUT, BROWN TROUT, AND RAINBOW TROUT

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Abstract

Sulfonamides such as sulfisoxazole (Gantrisin^R), sulfamerazine, and a mixture of sulfamerazine with sulfaguanidine were fed to apparently normal fingerlings of brook trout (*Salvelinus fontinalis*), brown trout (*Salmo trutta*), and rainbow trout (*Salmo gairdneri*). None of these drugs had any growth-affecting influence on rainbow trout. Growth of brook trout was somewhat retarded by sulfamerazine. The retardation of the growth of brown trout was greater with sulfamerazine than with the mixture of two sulfonamides. Sulfisoxazole did not retard growth of any of the three species. As soon as the medicated food was replaced with normal, brown trout resumed growth. Observations are also furnished on the tissue levels of sulfonamides and hemoglobin in the experimental trout.

Introduction

A desirable chemotherapeutic agent should stop development or, even better, should kill the pathogens in tissues of the infected animal or plant and should be relatively harmless to the host. Unfortunately such "ideal" drugs do not exist, and the margin of safety varies with different agents, depending on the species treated.

Since sulfonamides are used widely in the treatment of bacterial fish diseases, one should bear in mind the observation that" . . . . there are no drugs of which more side-effects are mentioned in the literature than the sulfonamides" (Meyler, 1952). Highly specific reactions to sulfamerazine have been shown in brook trout, brown trout, and rainbow trout (Gutsell and Snieszko, 1949). Johnson and Brice (1953) observed a toxic effect of sulfamerazine to fingerling coho salmon (*Oncorhynchus kisutch*). Earp, Ellis, and Ordal (1953) reported that treatments with sulfadiazine or sulfamethazine were apparently harmless to spring chinook salmon (*O. tshawytscha*) and sockeye salmon (*O. nerka*). Therefore the effects of sulfonamides, or other drugs, on fishes should be determined before they are used for the therapy of various bacterial diseases.

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The studies reported here were carried out to determine the effect of certain sulfonamides on the growth rate of three species of trout. Sulfisoxazole was tested because of its lack of toxicity to poultry (Tabenkin, *et al.*, 1953), and for its effectiveness in the treatment of kidney disease in brook trout (Snieszko and Griffin, 1955). A mixture of sulfamerazine with sulfaguanidine was superior to sulfamerazine alone in the treatment of furunculosis in brown trout (Flakas, 1950). Sulfamerazine was included to permit a close comparison of the results with those of Gutsell and Snieszko (1949). Any substantial difference between the present results and those obtained by Gutsell and Snieszko would support the belief that the response was lot- rather than species-specific. In case of such lot-specificity, further research of this type would have little significance, whereas proof of a constant species-specifity of the effects of various sulfonamides on fishes would be of considerable practical importance.

MATERIALS AND METHODS

Fingerling brook, brown, and rainbow trout were distributed in 500-gram quantities among experimental troughs. The following treatments were selected: 1. sulfamerazine, 2. sulfamerazine 6 parts and sulfaguanidine 4 parts; 3. sulfisoxazole (Gantrisin^R)[4]; 4. controls (no medication). All drugs were administered with food at a rate of 200 milligrams per kilogram of fish per day. The drugs were mixed first with the dry portion of the diet and then added to the meat. The full diet consisted of 25 percent dry mixture and 75 percent meat. The dry mixture was made of equal parts by weight of cottonseed meal, fish meal, distiller's solubles, wheat middlings, and 4 percent table salt. Meat consisted of equal parts of beef liver and beef spleen. Food was given twice daily; the rate was 8 percent of the weight of trout per day. There was only one feeding on Sundays, thus the fish received half of the daily ration on that day. All tests were made in duplicate. Water temperature was 12.2° C. (54° F.).

The experiment was started on April 12 and finished on July 12, 1954. Fish were weighed at 2-week intervals. Following each weighing, fish in excess of 500 grams were removed. After 8 weeks, the experiment was terminated with brook trout and rainbow trout, but was continued with brown trout, the species most affected by the treatments. During the ninth week hemoglobin and the tissue levels of sulfonamides were determined in 5 trout selected at random from each trough.

At the end of the ninth week the brown trout fingerlings in each pair of troughs receiving the same treatment were pooled and distributed in 220-gram quantities into four experimental troughs. Trout in two of these troughs remained on the medicated diet and the other half received the same food without sulfonamides. The purpose of this test was to determine whether fingerling brown trout stunted on the diet containing sulfamerazine, and sulfamerazine with sulfaguanidine, would resume normal growth on a food free from these drugs. The experiment with these brown trout was continued for an additional 4 weeks (total, 13 weeks).

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[4] Furnished free of charge by Hoffmann-La Roche, Inc., Nutley, N. J.

Trout selected at random from each trough were used for histological examination and determination of the tissue concentration of sulfonamides and hemoglobin. To minimize the danger of contamination by regurgitated food when fish were killed, trout did not receive any food during the 24 hours prior to examination. The intestinal tract was removed. Fish were ground in a Waring blender with distilled water and the sulfonamides determined in an electric colorimeter by the method of Bratton and Marshall (1939) as described by Levinson and MacFate (1946).

EFFECTS ON GROWTH

The effect of sulfamerazine on the growth of all three species of trout (Table 1; Fig. 1) was of the same nature as reported by Gutsell and Snieszko (1949). The growth rate of rainbow trout was not affected, but in brook trout growth was reduced about 30 percent during the 8 weeks. The greatest effect occurred in brown trout which showed growth about 450 percent greater in the controls than in the fish receiving sulfamerazine. These results indicate that the reaction to sulfamerazine in brook, brown, and rainbow trout fingerlings is species-specific and apparently of the same magnitude in different lots of fish tested at intervals of several years. It is strongly probable that the effects of sulfisoxazole and the mixture of sulfamerazine with sulfaguanidine are also species-specific and that the results

TABLE 1.—*Response, expressed as percentage gain in weight, of normal fingerling brook, brown, and rainbow trout to a diet containing several sulfonamides administered at a rate of 200 milligrams per kilogram of fish per day*

Sulfonamide and species of trout	Average percentage gain per two troughs by 2-week periods				Total percentage gain per trough April 12–June 7		Total mortalities per treatment
	1	2	3	4	A	B	
Sulfisoxazole							
Brook trout	55	36	42	39	178	166	5
Brown trout	40	33	30	28	132	130	4
Rainbow trout	38	38	34	27	138	136	2
Sulfamerazine							
Brook trout	41	26	25	21	112	114	5
Brown trout	16	5	8	0	24	34	17
Rainbow trout	30	26	36	38	128	132	4
Sulfamerazine with Sulfaguanidine							
Brook trout	39	30	31	28	140	116	6
Brown trout	28	8	10	3	44	54	17
Rainbow trout	31	28	27	29	118	112	0
Controls							
Brook trout	48	43	36	32	164	154	5
Brown trout	44	37	34	25	138	142	8
Rainbow trout	34	34	34	31	136	130	4

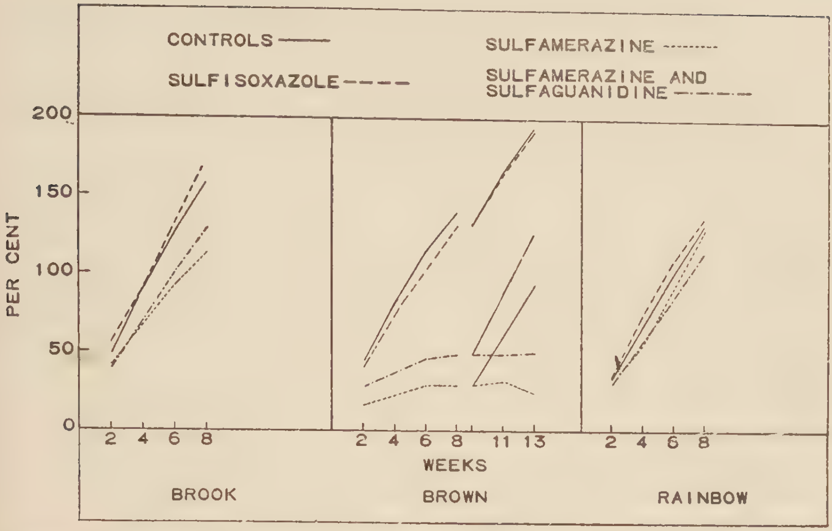

FIGURE 1.—Growth of three species of fingerling trout fed diet containing 200 milligrams of sulfonamides per kilogram of fish per day as compared with growth of controls receiving the same diet but without sulfonamides.

can reasonably be applied to other treatments of the same species of trout with the same drugs.

The growth rate of brook and brown trout treated with a mixture of sulfamerazine and sulfaguanidine was somewhat better than that of the fish receiving sulfamerazine. The difference may explain why an outbreak of furunculosis in brown trout responded more favorably to treatment with the above-mentioned mixture than with sulfamerazine alone (Flakas, 1950).

Sulfisoxazole had only a slight growth-retarding effect on brown trout and appeared even to stimulate the growth of brook and rainbow trout.

The strong growth-retarding effect of sulfamerazine alone or with sulfaguanidine on brown trout was apparently due to a gradual loss of appetite in the treated fish. From the second week brown trout nearly stopped taking food containing these sulfonamides. So much food was left over in the troughs that it is surprising that any growth took place and that sulfonamides were present in the tissue extract. When the medicated food was replaced after 9 weeks with normal diet, the growth rate of brown trout returned to normal (Fig. 1; Table 2). This observation as well as the lack of any pathological changes in the treated brown trout seems to indicate that in this species sulfamerazine alone or with sulfaguanidine causes some physiological upset which gradually reduces the appetite. If refusal to take food were abrupt and displayed also by brook trout and rainbow trout, one could suspect that aversion to the medicated diet was caused by its taste. Slight loss of appetite was also noticed in

TABLE 2.—*Growth and mortality of fingerling brown trout maintained for 13 weeks on a diet containing sulfonamides, and growth of fish fed the medicated diet for 9 weeks followed by a normal diet for 4 weeks*

[All fish received medication, April 12–June 14. Troughs were standardized at 220 grams each on the latter date. Beginning June 14, medication was terminated for two lots but was continued for two others. Duplicate lots are indicated as A and B]

Item	Average number of trout per trough June 14	Percentage gain or loss per trough June 14–July 12		Number of mortalities per trough June 14–July 12	
		A	B	A	B
Sulfisoxazole					
With drug, April 12–July 12	32	+60	+63	..	..
Without drug, June 14–July 12	31	+61	+67	..	..
Sulfamerazine					
With drug, April 12–July 12	72	− 5	− 6	7	9
Without drug, June 14–July 12	61	+65	+66	2	..
Sulfamerazine with Sulfaguanidine					
With drug, April 12–July 12	64	− 6	+ 9	6	2
Without drug, June 14–July 12	63	+69	+84	..	..

brook and rainbow trout receiving sulfamerazine alone and in a mixture with sulfaguanidine. No reduction of appetite, as compared with the controls, was noticed in any trout given sulfisoxazole.

The barely perceptible growth-stimulating effect of sulfisoxazole on brook or rainbow trout is so small that it has no practical importance. It may have occurred due to control of some low-grade infection.

In the determination of sulfonamide levels in the tissues of experimental trout, the lowest readings were found in trout treated with Gantrisin (Table 3). This observation is in agreement with our preliminary test which indicated that tissue levels of sulfisoxazole in brook trout decrease rapidly. This is also true in humans where "the higher rate and rapidity of elimination of the drug explain the low levels attainable in the blood and body fluids" (Sophian, Piper and Schneller, 1952, p. 57).

Hemoglobin levels of control fish were perceptibly lower in brown trout than in brook or rainbow trout. The hemoglobin contents increased by about 10 percent in brook trout receiving sulfamerazine and in brown trout

TABLE 3.—*Concentration of sulfonamides (milligrams per 100 grams of fish) in the tissues of experimental trout*

[Each reading represents a composite sample of 10 trout. The last feeding of medicated food was given 24 hours before the determinations were made on June 9, 1954]

Species	Sulfisoxazole	Sulfamerazine	Sulfamerazine and sulfaguanidine[1]
Brook trout	...	3.8	3.0
Brown trout	0.8	2.1	1.2
Rainbow trout	0.9	6.6	4.1

[1] The drugs were in the ratio of 6 parts of sulfamerazine to 4 parts of sulfaguanidine. The concentration was calculated on the basis of the tissue levels as previously determined for both sulfonamides separately (Snieszko and Friddle, 1951)

treated with the mixture of sulfamerazine and sulfaguanidine. No significance would be attached to this observation if it were not in general agreement with observations reported earlier by Gutsell and Snieszko (1949) and Gutsell (1951).

Histological examination revealed no tissue damage in the kidneys or other organs regardless of the species of trout or type of sulfonamide. More detailed histopathological observations will be reported elsewhere (Wood, Yasutake, and Snieszko, 1955).

The possibilities of sulfisoxazole in the therapy of fish diseases have so far been tested only (and with good results) in the treatment of kidney disease in brook trout (Snieszko and Griffin, 1955). The observation that this drug has no growth-depressing effect on any species of trout is especially promising for the therapy of bacterial diseases of brown trout, since growth of this species is greatly depressed by sulfamerazine alone or in a mixture with sulfaguanidine. In the lower warm-blooded vertebrates as in the chickens (Tabenkin, *et al.*, 1953) no evidence of toxicity was observed after feeding a diet containing a high concentration of sulfisoxazole. In fact, as in fishes, (Table 1, Fig. 1) this drug was observed to stimulate growth if added to the chicken diet in concentrations of 0.03 to 1.0 percent.

Until it becomes known how effective sulfisoxazole will be in the treatment of trout suffering from other bacterial diseases than the kidney disease, it should be used on the experimental basis only. Caution is recommended since it is well known that chemotherapeutic agents are species-specific in regard to their side effects on the hosts and the control of pathogenic bacteria. Therefore results obtained in the treatment of one disease in one species of fish can not be generalized without experimental support.

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THE KILLIFISH, FUNDULUS HETEROCLITUS, SECOND INTERMEDIATE HOST OF THE TREMATODE, ASCOCOTYLE (PHAGICOLA) DIMINUTA

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Ascocotyle (*Phagicola*) *diminuta* was described by Stunkard and Haviland (1924) from the intestine of wild rats collected at the Clason Point dump near New York by the City Board of Health. Feeding experiments have demonstrated that metacercariae encysted in the gills of the common killifish, *Fundulus heteroclitus,* are stages in the life-cycle of this parasite. The larvae have been found also, although rarely and in small numbers, in the gills of the striped killifish, *Fundulus majalis.* Since both species of *Fundulus* are susceptible, it appears probable that the habits of *F. heteroclitus* occasion greater exposure of this species to the cercariae. It is possible that infection of the fishes occurs during the spawning season when they are in water of low salinity. The asexual stages of these trematodes and the mollusks which harbor them are yet unknown.

When Stunkard and Haviland described *A. diminuta,* they divided the genus *Ascocotyle* Looss, 1899 into two subgenera, *Ascocotyle* and *Parascocotyle,* with *A. coleostoma* (Looss, 1896) type of the genus as type of the subgenus *Ascocotyle* and *A. minuta* Looss, 1899 as type of the subgenus *Parascocotyle.* The two species appeared to differ significantly but the subsequent discovery and description of a number of additional species have disclosed intermediate conditions that seem to bridge the differences between the subgenera. Previously Faust (1920) had described worms from the intestine of the monkey-eating eagle of the Philippine Islands, *Pithecophaga jefferyi,* as members of a new genus and species, *Phagicola pithecophagicola.* According to Faust, "A close study of *Phagicola pithecophagicola* shows it to belong to a group possessing in part the characters of the Brachycoelinae, in part those of the Microphallinae, in part those that are unique." Accordingly, a new subfamily, Phagicolinae, was erected to receive it. The diagnosis of the subfamily was of course merely a list of the characters of the genus *Phagicola.* Actually the description of the worms was very incomplete and in a subsequent publication, Faust and Nishigori (1926) there is the statement, "In 1920 one of us (Faust) described a new species from the intestine of the monkey-eating eagle under the name *Phagicola pithecophagicola,* a fluke which on restudy has been found to belong to the genus *Ascocotyle* and should, therefore, be designated as *Ascocotyle pithecophagicola.*" Witenberg (1929) raised *Parascocotyle* to generic status and transferred several species from *Ascocotyle* to *Parascocotyle;* among them *P. pithecophagicola* Faust, 1920. Although he recognized *Parascocotyle* as a valid genus, Witenberg considered *P. diminuta* specifically identical with *P. mi-*

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nuta (Looss, 1899) from dogs, cats and *Ardea cinerea* of Egypt. The genus was included in the subfamily, Centrocestinae, of the family Heterophyidae. Examination of original specimens of *P. pithecophagicola* by Witenberg did not yield further information and he (1930) reported that redescription from more favorable material would be required to determine whether or not *Parascocotyle* is identical with *Phagicola.*

The status of *Phagicola* is still unsettled. Travassos (1930) adopted the opinion of Stunkard and Haviland and recognized the two subgenera in *Ascocotyle.* However, he suppressed *Parascocotyle* as a synonym of *Phagicola,* included all previously described species in the genus *Ascocotyle* and arranged them in the two subgenera, *Ascocotyle* and *Phagicola.* The species of Faust was listed as *Ascocotyle* (*Phagicola*) *pithecophagicola. Ascocotyle* (*Phagicola*) *diminuta* was recognized as a valid species. Price (1932b) reported briefly on a re-examination of the type specimens of *Phagicola pithecophagicola.* He found the postoral appendage, which extended to the pharynx, two gonotyls in the genital sinus, and a globular seminal receptacle median to the ovary. With the description of these features, the first two of which were overlooked in the original description, Price announced the identity of *Phagicola* and *Parascocotyle.* He considered the differences between *Ascocotyle* and *Phagicola* to be of generic significance. Price (1932c) described two new species of *Ascocotyle* from the intestine of *Butorides* sp. taken in Puerto Rico, and reported finding *Phagicola diminuta* in the same host. Price (1933a) studied the original specimens and revised the description of *Ascocotyle plana* Linton, 1928 a species, taken from *Butorides virescens* at Woods Hole, Massachusetts, which had been regarded by Witenberg (1929) as identical with *Pygidiopsis genata* Looss and by Travassos (1930) as identical with *Ascocotyle* (*Phagicola*) *angrense* Travassos, 1916 from *Butorides striata, Butorides virescens,* and *Butorides erythromelas* of South America. The specimens were referred to the genus *Pygidiopsis* as *P. plana* (Linton, 1928). Price (1933b) published new host records for trematodes of the genus *Phagicola. Phagicola nana* (Ransom, 1920), originally described as *Ascocotyle nana* from the Alaskan fox, *Vulpes lagopus,* was reported from a booby bird, *Sula bassana.* In this species Price noted that the oral coronet consists of "a complete anterior row of 16 spines and an incomplete posterio-dorsal row of 3 to 4 spines." The specimens of *P. longa* (Ransom, 1920) from *Vulpes lagopus* were compared with Witenberg's description of this species from the dog, cat, and Persian wolf. According to Price, Ransom's material showed many abnormalities and the specific description was emended; Price reported *P. longa* also from an undetermined species of pelican. Ciurea (1933) described heterophyid parasites from mammals and birds, obtained by feeding fishes from the Danube and the Black Sea. After feeding metacercariae from the gills and superficial muscles of *Mugil capito* from the Black Sea to the dog and common cormorant, *Phalacrocorax carbo,* he obtained specimens presumably identical with those identified as *Parascocotyle longa* (Ransom, 1920) by Witenberg (1929). He noted that in these worms the acetabulum is located within the genital sinus and accordingly they were described as *Metascocotyle witenbergi* n. g., n. sp. Price (1935) described *Ascocotyle tenuicollis* n. sp. and published more extended descriptions and figures of *Ascocotyle megalocephala* Price, 1932, *Ascocotyle puertoricensis* Price, 1932 and of *Phagicola pithecophagicola* Faust, 1920. He stated that the location of the acetabulum within the genital sinus is common to all members of *Phagicola* and *Ascocotyle,* and accordingly the genus *Metascocotyle* Ciurea was suppressed as identical with *Phagicola*. Price disagreed with the opinion of Travassos (1930) that *Phagicola* should be considered a subgenus of *Ascocotyle*. As generic distinctions he stated, "Members of the genus *Ascocotyle* have 2 rows of spines in the oral coronet; the cuticula is entirely covered with spines; the uterus extends anterior to the genital aperture; and the vitellaria extend anterior to the level of the ovary. Members of the genus *Phagicola* have only a single row of spines in the oral coronet; the cuticular spines are absent at the posterior end of the body; the uterus does not extend anterior to the genital aperture; and the vitellaria are confined to the post-ovarial region of the body." Srivastava (1935) reviewed earlier work on the genus *Ascocotyle* and described *Ascocotyle* (*Phagicola*) *intermedius* from the Indian fishing-eagle, *Haliaeetus leucoryphus*. The specific name was selected because in certain respects the worms were intermediate in structure between *Ascocotyle* and *Phagicola*. They have a double row of oral spines and the vitellaria extend to the level of the pharynx, but the uterus does not enter the preacetabular zone. Accordingly, Srivastava reduced *Phagicola* to the rank of a subgenus and revised the diagnosis of *Ascocotyle* to contain the species formerly included in *Phagicola*. Price (1936) described *Ascocotyle mcintoshi* n. sp. from the white ibis, *Guara alba,* taken at Cape Sable, Florida. Commenting on the action of Srivastava, he argued that *Phagicola* is a valid genus since, "the species comprising the *Ascocotyle-Phagicola* complex fall quite distinctly into 2 categories—one group, *Ascocotyle,* having 2 rows of spines in the oral coronet, body completely spined and vitellaria extending anterior to the level of the ovary, and the other group, *Phagicola,* having a single row of spines in the oral coronet, the body incompletely spined (spines absent on posterior portion of body) and vitellaria confined to the postovarial region. In view of the fact that in each of these groups there are at least 3 correlated characters the writer regards *Ascocotyle* and *Phagicola* as better established genera than some of the other genera of heterophyids, as well as many genera of other families, the validity of which rests largely upon a single character which in many cases is decidedly variable." It is to be noted that Price (1936) had dropped the extent of the uterus as a generic character and there is doubt concerning the significance of the number of rows of oral spines. He (1933b) had reported that in *Phagicola nana* there is "a complete anterior row of 16 spines and an incomplete posteriodorsal row of 3 to 4 spines." We have found that in *Ascocotyle* (*Phagicola*) *diminuta* there are two dorsal spines of a second row. It appears, therefore, that in these species a second row is represented by a few persistent spines. If these spines are actually members of a second incomplete row of smaller spines, and in species of *Ascocotyle* the spines of the second row are smaller than those in the anterior row, the distinction between *Ascocotyle* and *Phagicola* rests on the extent of body spination and of the vitellaria. Moreover, the figure of *Ascocotyle puertoricensis,* published by Price (1935), shows that the vitellaria extend only a very short distance anterior to the ovary and do not reach the level of the genital aperture. Decision on the taxonomic status of *Phagicola* should await more complete information, especially on the developmental stages of its members.

Nishigori (1924) reported the life-cycle of *Stamnosoma formosanum,* a species which Price (1932a) transferred to *Centrocestus* on suppression of the genus *Stamnosoma* Tanabe, 1922. Yamaguti (1938) described the life-history and developmental stages of *Centrocestus armatus* (Tanabe). The asexual stages occur in species of *Semisulcospira,* the metacercariae in the gills of the freshwater cyprinid, *Pseudorasbora parva,* and the adults in *Milvus migrans lineatus.* Price (1940) gave a synopsis of the superfamily Opisthorchioidea Vogel, 1934 and discussed the adult morphology as well as the life-cycles and cercarial types of twenty species for which information was then available. Four families were recognized in the superfamily; two of them, Opisthorchiidae Braun, 1901 and Heterophyidae Odhner, 1914, contain species which are parasitic chiefly in warm blooded hosts and the others, Acanthostomidae Poche, 1926 and Cryptogonimidae Ciurea, 1933, contain parasites which usually occur in cold blooded hosts. Diagnoses were given for families and subfamilies, with lists of genera included in each. *Ascocotyle* and *Phagicola* were placed in the subfamily Centrocestinae, family Heterophyidae. Price stated that all described cercariae are pleurolophocercous or parapleurolophocercous but noted unexpected differences in the excretory systems of the cercariae which are unlike in shape of bladder, pattern of excretory ducts, and flame-cell formulae. It should be pointed out that the cercaria of *Centrocestus armatus* differs from other pleurolophocercous larvae in the absence of a caudal fin. Cable and Hunninen (1942), after describing the developmental stages of *Siphodera vinaledwardsi,* a member of the Cryptogonimidae, listed features common to the Heterophyidae, Cryptogonimidae and Acanthostomidae. All of the heterophyid cercariae are similar and it is probable that the as yet unknown cercaria of *Ascocotyle* (*Phagicola*) *diminuta* will prove to be a member of this larval group.

The original description of *Ascocotyle* (*Phagicola*) *diminuta* was made from moribund specimens found in the washings of the intestines of two rats that had been kept for several days in refrigeration. As a result, the account lacked precision in certain respects, especially the number of oral spines, and measurements made on such material may not be typical of normal individuals. It is recognized that trematodes, moribund in the intestines of their hosts or in the fluid of dissection, tend to relax and absorb water. Discovery of the metacercariae and experimental infections of rats, mice, hamsters, gulls (*Larus argentatus*) and a night-heron (*Nycticorax nycticorax*) have provided an abundance of vigorous, active worms. Accordingly it is possible to make additions and emendations to the description of the species.

The metacercariae were discovered by Uzmann in the gills of *Fundulus heteroclitus* collected in areas near the laboratory of the U. S. Fish and Wildlife Service at Milford, Connecticut. Examination of encysted specimens and others released from their cysts disclosed the resemblance between these worms and those described by Stunkard and Haviland (1924) from the rat. Feeding gills of *F. heteroclitus* to rats and mice yielded adult worms identical with those described earlier from natural infections. Gills of *F. heteroclitus* collected from the Clason Point area near New York and from Chesapeake Bay near Annapolis, Maryland, showed cysts of the same parasite. The incidence and intensity of infection varied little in fishes from different locations. Eighty-eight to ninety-six per cent of the fishes taken near the laboratory at Milford, Conn., harbored metacercariae and total counts made on twenty-five fishes varied from 0 to 218, with an average of 56 cysts per fish. Although *F. heteroclitus* bore heavy infections, examination of twenty-five *Fundulus majalis* from the Milford region showed only five of them infected and the number of cysts varied from one to eleven.

Cysts in the gills of *Fundulus* (Fig. 1) are oval and measure from 0.07 to 0.14 mm. in width and from 0.13 to 0.22 mm. in length. The cyst wall is composed of a thin, flexible and very tough membranous envelop, surrounded by a connective tissue capsule. The worms grow in their cysts; in smaller cysts they may not entirely fill the space and are not folded, whereas in mature cysts (Fig. 2) they are much larger and the body is doubled on itself. Excysted specimens, when extended, measure 0.116 to 0.33 mm. in length. In young cysts the larvae have small eye-spots, but in older ones the pigment is dispersed. The spines of the oral coronet increase in size as the larvae grow; they are visible in the cyst and provide a useful identifying character. The intestinal ceca of small metacercariae contain erythrocytes of *Fundulus,* and they may persist for some time. Metacercariae from fishes that had been kept in captivity for three months, during which time they had not been exposed to cercariae, had red blood cells in their digestive ceca. It appears that in penetrating the gills, the cercariae break the capillary beds and come to lie in small pools of blood. Blood must be ingested either before or after encystment and the red cells are not digested by the larvae. Eventually they decompose and disappear and they are not present in large metacercariae.

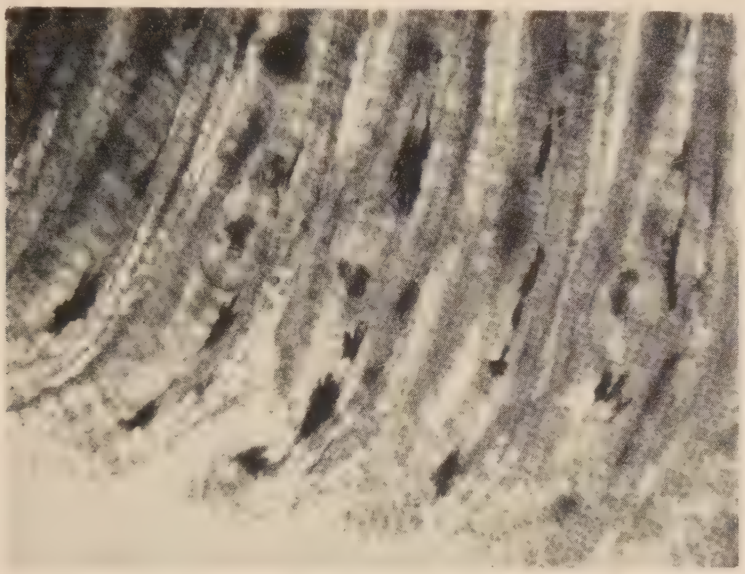

FIGURE 1. Photomicrograph, gills of *Fundulus heteroclitus,* showing encysted metacercariae of *Ascocotyle* (*Phagicola*) *diminuta.*

Gills were fed to rats, mice, hamsters, chicks, young laboratory raised gulls (*Larus argentatus*) and to a black-crowned night-heron (*Nycticorax nycticorax*).[2] All of these animals except the chicks, which proved refractory, were susceptible to infection and gravid worms were recovered in large numbers. The first rat, fed gill arches and filaments from five fishes each day for three days (Feb. 24, 25,

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[2] This bird, a young female, was trapped in Bronx Park and provided through the cooperation of the New York Zoological Society.

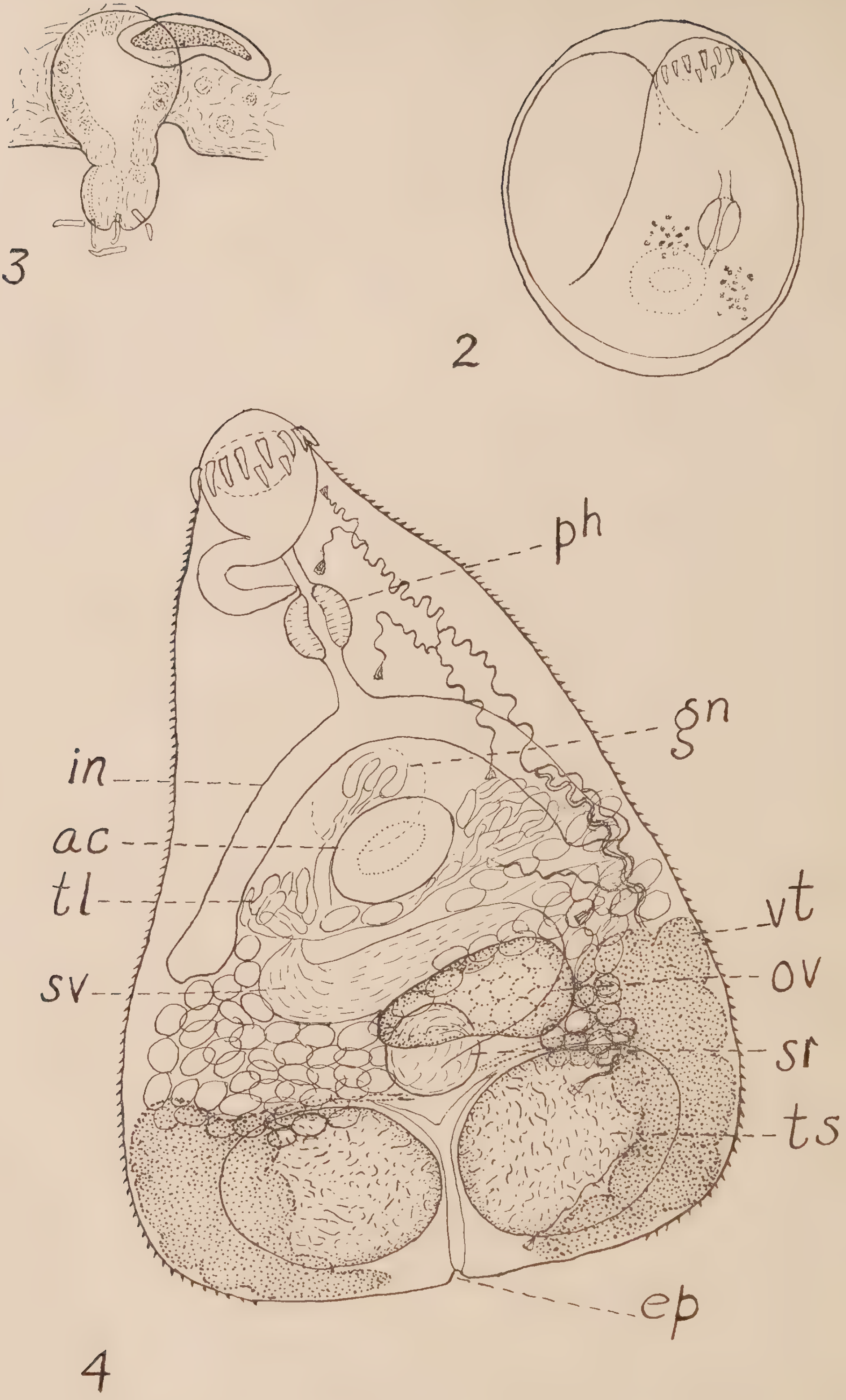
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Plate I

26, 1953) and killed four and one-half days after the first feeding, yielded over three hundred specimens, most of them sexually mature. Another rat, fed gills from four fishes on March 12 and from three fishes on March 14, was killed on March 23 and contained several hundred worms, all of them filled with eggs. A mouse killed two days after a single feeding contained almost one hundred worms, none of them with eggs. It appears that the worms may develop sexual maturity in three days, but worms from the smaller and younger cysts, although infective, require a longer time, as much as a week, to become mature, and they mature at a smaller size. Gills from two fishes were fed to a hamster and 253 gravid worms were recovered when the animal was sacrificed one week later. *Fundulus* were fed to laboratory-raised *Larus argentatus* which became infected. Also, six fishes were fed to a night-heron, *N. nycticorax,* and the bird was killed two days later. It contained about one hundred sexually mature worms of a natural infection and more than one hundred immature worms of the experimental feeding.

The worms recovered from the experimental infections of rats are more compact and robust than those from natural infections described by Stunkard and Haviland (1924). The specimen shown in Figure 4 is typical; it is one of the largest and as stained and mounted measures 0.31 mm. in length. In general, the worms are somewhat larger, with much larger gonads. Mature specimens vary from flask-shaped to triangular in outline, and the body is somewhat concave ventrally. The postacetabular portion, filled with reproductive organs and eggs, is much thicker than the more mobile anterior part of the body. The coronet of oral spines consists of a single row of sixteen spines and two additional spines, somewhat smaller than those of the complete row, situated on the dorsal side, immediately behind and on either side of the central spine. The flattened scale-like spines of the cuticula are absent from a narrow postoral zone or band and from the extreme posterior end of the body. The pigment from the eye-spots of the cercariae persists as dispersed granules in gravid worms. The degree of extension in the anterior part of the body determines the relative position of the oral appendage and the pharynx. When extended, the oral cecum may terminate some distance anterior to the pharynx as shown in the figure by Stunkard and Haviland, but when the body is contracted, as shown in Figure 4, the oral appendage may overlap the pharynx. The excretory system has been worked out in living worms and is depicted on the right side of Figure 4. The pore is terminal and the excretory vesicle is V-shaped with a short duct from the point of the V to the exterior. The two arms of the vesicle are dorsal and anterior to the testes and tend to follow their contour. When filled and compressed, the vesicle becomes reniform, overlying the

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FIGURE 2. Encysted metacercaria of *A. diminuta* from gills of *F. heteroclitus,* showing the coronet of oral spines, pharynx, acetabulum, and dispersed pigment of the larval eye-spots.

FIGURE 3. Portion of a transverse section of *A. diminuta,* showing everted gonotyl and spines. At the upper right of the figure there is a collapsed egg with contained miracidium.

FIGURE 4. Mature specimen of *A. diminuta* from the intestine of a rat; dorsal view, experimental infection, egg shells collapsed in the terminal loop of the uterus; abbreviations,

ac	acetabulum
ep	excretory pore
gn	gonotyl
in	intestine
ov	ovary
ph	pharynx
sr	seminal receptacle
sv	seminal vesicle
tl	terminal loop of uterus
ts	testis
vt	vitellaria

testes with the ends of the vesicle extending almost to the lateral margins of the body, and anteriorly almost to the ends of the digestive ceca. On either side a collecting duct arises at the lateral end of the vesicle and extends forward in a sinuous course. A short distance anterior to the level of the acetabulum it divides into anterior and posterior branches, each of which bears two pairs of flame cells (Fig. 4). The arrangement of the flame cells on the posterior branch is the reverse of that on the anterior branch and the flame cell formula is $2[(2+2)+(2+2)]$. Counting backward from the anterior end, the first pair of flame cells is slightly ventral in position at the sides of the oral sucker; the second pair is dorsal in position anterior and lateral to the pharynx; the third pair is ventral, posterolateral to the pharynx; and the fourth pair is dorsal, preacetabular, above the digestive ceca. The fifth pair is ventral, lateral and slightly posterior to the acetabulum; the sixth pair is dorsal at the preovarial level; the seventh pair is dorsal, above the anterior edge of the testes; and the eighth pair is ventral, behind and below the testes. In the original report the relation between the acetabulum and the genital sinus was described but the gonotyl was not observed. In the more favorable material the gonotyl is recognizable but it assumes different shapes and is protrusible as shown in a transverse section (Fig. 3). The gonotyl bears very small spines, probably six in number, but they do not show well in whole mounts.

Other differences between present specimens and the original account are noted in the size of the gonads. It is clear that the specimens from which the original description was made were in very poor condition. In the experimentally produced worms the testes are large, the medial faces are in contact or even overlapping; the ovary is much larger, ovate in shape with the wider end lateral in position. The course of the uterus has been traced by following eggs as they passed along. As noted in the original description, the oviduct arises at the median posterior margin, the ootype is lined with long, rapidly beating cilia, the initial course of the uterus is posteriad on the right side of the seminal receptacle forming a loop along the anterior edge of the right testis, then forward to the right edge of the body, thence directly across to the opposite side where there is a posterior loop along the anterior face of the left testis, then across to the right side of the body where there is another loop and the uterus then crosses to the left side and forms another loop before the metraterm opens into the genital sinus. The eggs in the initial portion of the uterus have clear, transparent shells; as they pass along the shells become darker in color and those in the terminal loop are bright yellow. The eggs in the terminal coils of the uterus contain miracidia and eggs removed from gravid worms were kept under observation. Movement of the larvae was observed, but none of them emerged. Eggs were not recovered from the feces of infected rats, mice or hamsters, although gravid worms were found in the intestine of a rat killed six weeks after it was infected.

Measurements in millimeters of fixed, stained and mounted specimens are: length, 0.2–0.44; width, 0.11–0.24; diameter of oral sucker, 0.025–0.042; pharynx, 0.019–0.025; acetabulum, 0.03–0.04; testes, 0.03 by 0.04 to 0.05 by 0.07; ovary, 0.03 by 0.04 to 0.035 by 0.056; eggs, 0.016 by 0.010 to 0.02 by 0.011.

Sexual development of animals is dependent on nutritional and other physiological factors and its extent is often anomalous or irregular in parasitic worms from abnormal hosts. The variations in the degree of sexual maturity of *Ascocotyle diminuta* in mammals and the failure to recover eggs of the parasite in the feces of these hosts suggest that the natural hosts are piscivorous birds. Price reported the species from *Butorides* sp. and we have found it in *Nycticorax nycticorax*. These herons are common in the Milford area and feed in creeks where *Fundulus* is abundant.

SUMMARY

The metacercarial stage of *Ascocotyle* (*Phagicola*) *diminuta* Stunkard and Haviland, 1924 has been found encysted in the gills of *Fundulus heteroclitus*. Experimental infections of rats, mice, hamsters, *Larus argentatus* and *Nycticorax nycticorax* have yielded adult worms and permitted additions and emendations to the description of the parasite.

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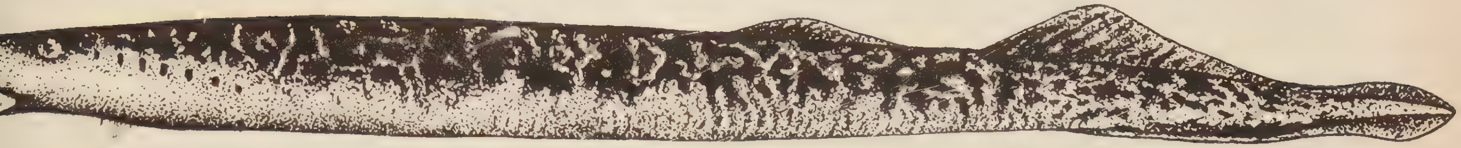


# of the Great Lakes

Will fishing industry survive the sea lamprey?

Paul E. Thompson

A HUNDRED AND TWENTY-FIVE YEARS AGO a group of Canadian engineers, steamboaters, and freighters stood triumphant beside the newly completed Welland Canal—a monument to human skill and endurance. Now ships from the growing Great Lakes mining, industrial, and fishing ports could skirt Niagara Falls, formidable navigation barrier on the route to the Atlantic. But as with many man-made "creations," that marvelous engineering feat had other far-reaching but disastrous effects its builders could not foresee. For Niagara Falls, between Lake Ontario and Lake Erie, had barred admission of an ugly, slithering parasite called the sea lamprey. By unleashing this blood-sucking Dracula, the Canal was ultimately to upset the delicate balance of nature and wreak havoc on a multi-million-dollar fishing industry.

Today the individual and local suffering is vividly apparent along the Huron and Michigan shores even to the casual visitor: beached and abandoned fishing boats, listed over and rotting; formerly busy and prosperous fish-buying houses fallen into neglect, with broken windows, sagging roofs, and unused wharves; forgotten net racks with bits of torn gillnetting whitening in the sun: and cottages forsaken by families gone to seek a living in the steel mills or the automobile industry after generations of fishing the lakes. A sad and desolate picture to those who love the water and its wealth, even though the heavily populated and highly industrialized Great Lakes states—New York, Pennsylvania, Ohio, Michigan, Indiana, Illinois, Wisconsin, and Minnesota—can easily absorb the loss of such an industry.

For centuries before the Welland Canal was even thought of, the parasitic eel-shaped lamprey moved each summer from the Atlantic Ocean into the coastal streams of Europe and North America to build nests, deposit eggs, and die. (They are the same creatures that are considered a delicacy in coastal Europe. An old story, apocryphal perhaps, has it that one of the food-loving British kings died after overindulgence in lampreys cooked in wine. A small relative of the sea lamprey is a native resident of Mexico.) Some on this side of the Atlantic long ago forsook the ocean forever and lived out their lives in Lake Ontario as dwarfs, feeding on resident fish, spawning and dying in its tributary streams.

History does not tell us when sea lampreys first moved into the Finger Lakes of New York State, but we are sure they came from Lake Ontario via the elaborate system of barge canals connecting Oswego with Buffalo. Students and teachers at Cornell University, just above Cayuga Lake, have used this Finger Lake as an outdoor biological laboratory, carefully observing the sea lamprey population. The typically dwarfed landlocked form averages only about twelve inches long and feeds indiscriminately upon all seventy-four species of fish in the lake. Even after a biological balance has been struck between prey and parasite, the lamprey annually kills more food fish, it is believed, than do all the fishermen on Cayuga Lake. As many as twelve out of fifteen catfish taken in some years have been heavily lamprey-scarred, and unknown thousands die of their wounds.

The mouth of this true sea monster is a nearly circular sucking disk, efficiently equipped with concentric rows of pointed teeth and an armored rasping tongue to grip the side of its victim and suck blood at leisure. A specialized gland secretes an anticoagulant to keep the blood flowing freely. Unless dislodged, the lamprey kills; if he does loose his hold for some reason, an ugly sore is left that sharply reduces the marketability of the host fish.

The lamprey at home in the sea may be three feet long; in the more restricted Great Lakes it is usually less than two feet, but is still a formidable enemy of many of our choicest fresh-water food fishes. Unfortunately, those lake-region residents who have eaten it have found it unpalatable, so that no demand for lampreys may be expected to reduce its numbers.

The sea lampreys have never really prospered in Lake Erie, a warm, shallow basin about 250 miles long, and it took almost a hundred years for them to traverse the lake and enter Lake Huron. This was the place for them, with cold waters, fat lake trout and delicious whitefish, and clear, gravel-bottomed tributary streams for spawning! They thrived, they spread, they ate their fill, and the work of engineers a century before came to dreadful fruition. From first penetration into Lake Huron in 1932, when the lake trout fishery yielded nearly two million pounds, until 1953, when less than fifty pounds were caught, the lampreys had their own way.

A Milwaukee, Wisconsin, fisherman brought in the first lamprey from Lake Michigan—next after Huron in the Great Lakes system—in 1936. It was sixteen inches long and attached to a four-and-a-half pound lake trout. From annual catches of five to six million pounds of these fine fish in the 1930's, Lake Michigan production sank to less than fifty pounds in 1953.

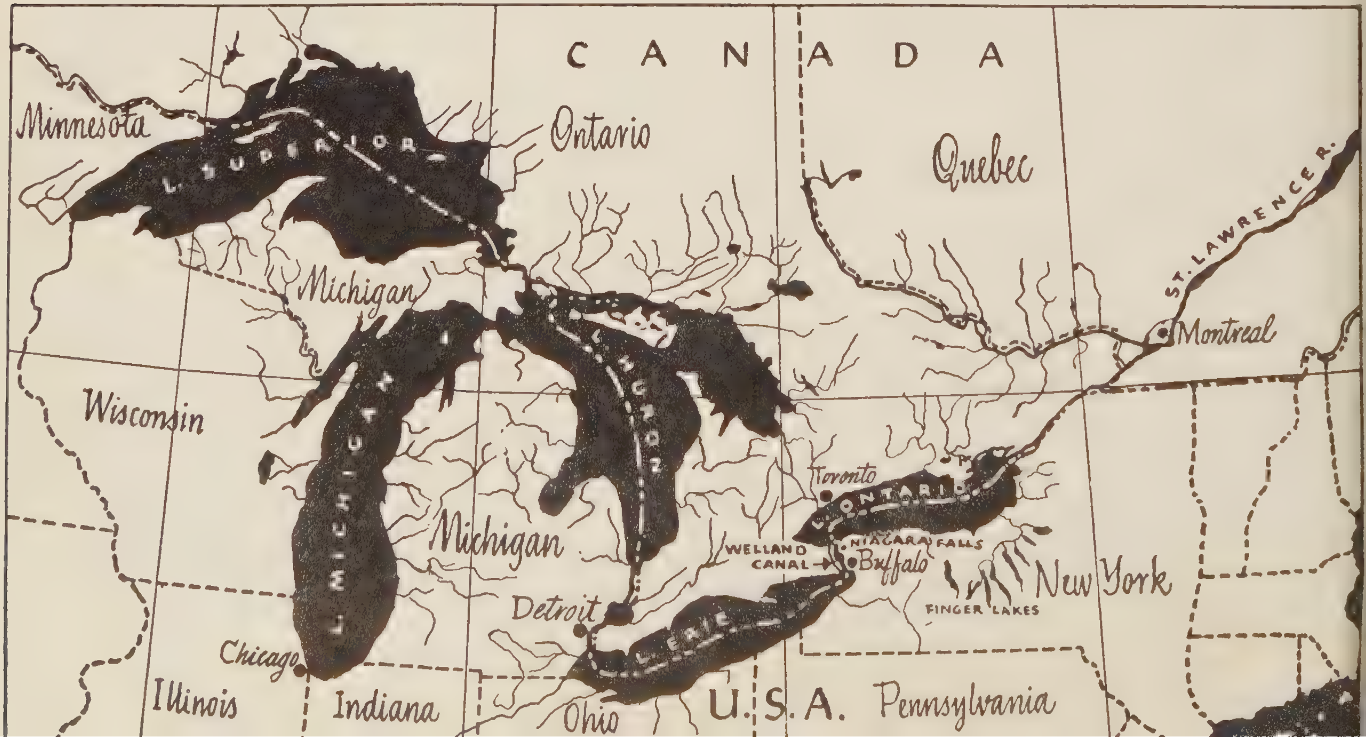
Lake Superior was invaded next, but not until 1947, and the full effect of the lamprey attack has not yet been felt in that huge, cold lake. Still, the history of the quick collapse of the lake trout fisheries of Lakes Huron and Michigan foreshadows the same tragedy in Lake Superior.

As usual in such cases, there were prophets of doom crying in the wilderness not very long after the first lamprey spawning migrant was discovered in the Huron River in 1932. That same year Dr. Charles W. Creaser of Wayne University in Detroit wrote with alarm in a national scientific journal: "In the not too distant future, it will no doubt be encountered throughout the Great Lakes waters. Knowing its record of destruction among the food fishes . . . , we must consider it as one more source of further depletion of the fisheries of the Great Lakes." Dr. Carl L. Hubbs, internationally known ichthyologist then at the University of Michigan, warned of the potential danger even earlier, in 1929, as more and more individual lampreys were picked up in Lake Erie, and again in 1936 after the first lamprey was reported in Lake Michigan. Dr. John Van Oosten, dean of Great Lakes fishery biologists for the United States Fish and Wildlife Service, warned the fishing industry of impending crisis.

Perhaps it is unfair to say these warnings went unnoticed, but certainly no widespread interest developed until after World War II. By that time fishermen around Lake Huron had caught many lamprey-scarred fish, their catches had fallen off alarmingly, and the State of Michigan decided to find out more about its new Public Fish Enemy No. 1. But by then there were more than sixty Michigan streams with established lamprey spawning runs and the Lake Huron lake trout catch had fallen to 173,000 pounds, one tenth of the catch a decade before.

In 1944 a fence and trap were placed in a Michigan stream and 3,366 lampreys were captured and killed during a part of the upstream spawning migration. Although this was a small-scale, inadequate operation, it did provide some information on the life history and habits of the parasite and a clue to its numbers, and gave impetus to greater research effort.

A lamprey-tight weir on the same stream in 1949 took 24,643 adults. Some of the early prophets of damage to the fisheries expressed doubt as to possibilities for control of the invading sea lamprey. Control, of course, essentially means deliberate overfishing. Many people interested in fishery conservation never hesitate to cry



depletion from overfishing" when a game or commer-ial fish is involved, even in these Great Lakes. But to et out purposefully to exterminate a species or reduce ts numbers to ineffectuality was a challenging task ndeed.

First, it was a question of our finding weak spots to ttack. Does the lamprey have enemies or parasites or liseases? No, apparently these were left behind in the ea. No doubt an abundance of food and lack of enemies ed to the fantastic success of this exotic in fresh water. Some aquarium experiments proved that American eels iked the flavor of young lampreys, but the idea of ntroducing another stranger into the lakes was rejected. We remembered what happened when the mongoose was ntroduced into the West Indies to kill off the snakes: the snakes are gone, but there are lots of mongooses and hey are crazy about domestic fowl. Sea lampreys don't ike the flavor of other lampreys, so cannibalism won't help. Does it move in schools like many fish so that it may be taken in quantity? No, in the lake it is a lone traveler, usually hitchhiking with a poor, unwilling fish. Can it somehow be prevented from reproducing? Yes, because it is most vulnerable in the shallow spawning streams on its upstream migration.

Physical barriers like the one illustrated are prohibitively expensive to build and maintain. They must be strong enough to withstand flash floods yet must permit free passage of water; they must be tended daily to clean away trash and remove and kill lampreys and pass food and game fish upstream from the traps. Fortunately, no more need be built. For cheap, easily installed electrical barriers are effective in killing the adult spawners without too much damage to food fishes in the same stream. The lampreys, less sensitive to electricity than other fish, run carelessly through a fringe of weak voltage into a strongly charged electrical field, where they are killed; desirable fish, on the other hand, are deflected by the weak impulses into an uncharged trap, from which they are easily transferred upstream. Experiments with alternating and direct current, different voltages and frequencies, and varying wave characteristics have established the efficacy and economy of control at this point in the lamprey's life history. An electrical fence costs about a fourth as much as a physical barrier does, and its operation costs only a few cents an hour for electricity.

After several years of observation and experimentation, we now know all the important elements of the lamprey's life history. They are primitive animals with a soft skeleton of cartilage rather than bone like their scaly-fish relatives. The spawning lampreys are highly sensitive to stream and stream-bottom conditions—they must have just the right temperature, strong water current, and coarse gravel for their nest-building. Hatching of the eggs—as many as 107,000 per female—takes two weeks. The baby lampreys are blind, toothless, and harmless. In a month or less the orphans (the parent lampreys die after spawning once) drift downstream and burrow into muddy bottom, passively sucking in whatever suitable food is brought to them by the currents. So they live for almost four years. Then when they are six or eight inches long, they gradually transform: eyes develop and the mouth evolves, growing rows of teeth and a rasping tongue. In fall and winter they move downstream to begin a parasitic life in the lake for eighteen months or so before the cycle is repeated. Carefully designed and controlled laboratory experiments continued for long periods have shown that no less than twenty pounds of fish is required to feed a parasitic sea lamprey to bring it to maturity.

Physical barriers to spawning lampreys, like this weir on the Ocqueoc River in Michigan, are expensive to build and tend

Newer, cheaper electrical weir kills lampreys trying to enter Hubbards Creek, Wisconsin, from Lake Michigan

This condensed account of the sea lamprey's birth, transformation, mode of living, spawning, and death suggests two important points to consider in reducing their numbers. At any one time there are four generations of the creatures snugly bedded in the streams awaiting transformation, plus juveniles and adults preying on fish in the lakes. Remove, then, all the adults as they move upstream to spawn in one season; replenishment will keep coming for four or five more years. The second point, also troublesome, is that the transformed, newly parasitic lampreys go foraging for the first time from their stream beds under cover of winter snow and ice in these northern waters, when it is difficult or impossible to capture or kill them.

Still another problem of considerable magnitude is the fact that we are dealing with no mere domestic difficulty. Only Lake Michigan is wholly within the United States; the shorelines of Lakes Erie, Huron, and Superior are shared with Canada. And the great, long-sought St. Lawrence River Seaway project, just authorized by the United States Congress, includes a plan for improving the old Welland Canal and its locks for ship traffic, so that lamprey traffic will no doubt benefit also.

What, then, is the outlook for the future?

We know from extensive surveys that lampreys inhabit ninety United States streams of Lake Superior, 107 of Lake Michigan, and thirty-three of Lake Huron. The Federal Fish and Wildlife Service and the states of Michigan and Wisconsin have seventy electrical and physical barriers to lamprey migration in operation in the three lakes, and the U.S. shore of Lake Superior will be completely blocked before the 1955 run. An intensive screening of new or little-known chemical compounds to find some that will kill the larval lampreys in their stream burrows without killing valuable fish has turned up several promising ones, though the probability of finding a highly selective lethal toxin seemed remote at the outset. If chemical control tests are successful and found practical for general application, the control process can be remarkably speeded up.

Concurrently with concern about the lampreys much advance planning is being done for fish restoration once control is achieved. Though some artificial propagation of fish has been disappointing from the standpoint of returns from hatchery plantings, we are hopeful about restoring lake-trout production in the Great Lakes. This big—up to a hundred pounds—flavorful fish is in great demand and often brings over a dollar a pound to the retail fish dealer. There are good reasons for optimism: hatchery-reared fish have been marked, planted, and recovered from the commercial fishery in encouraging numbers.

Plantings of lake trout in Lake Titicaca in Peru and Bolivia have been successful beyond expectation. In 1939 and 1940, 484,500 lake trout eggs were shipped from the U.S. fish hatchery at Cape Vincent, New York, by train, by steamer from New York City to Mollendo, thence by rail again to the lake, where they were hatched at Chucuito. This came about after Milton C. James, a fish-culture expert of the U.S. Fish and Wildlife Service, engaged in 1936 by a mixed Peruvian-Bolivian commission to study possibilities for increasing lake production, recommended importation of fertilized eggs. Despite the distance and the difficulties of transporting the lake trout eggs to Lake Titicaca at an altitude of over 12,500 feet, losses seem to have been small. Plans for shipment of more lake trout eggs were cancelled in 1942 because of war complications; nevertheless, there is no doubt that these fine fish have flourished and catches are made from both Peruvian and Bolivian shores.

Perhaps the brightest sign on the horizon is the prospect for early ratification and implementation of a fishery conservation treaty between the United States and Canada, which will make possible an all-out effort on an international scale to control this desperado. Already the Canadians have started an inventory of the problem on their side of the lakes, are laying plans for electrical devices in their streams, and are testing larvicides, too. The states involved and the Canadian province of Ontario are setting up the machinery for massive lake trout plantings.

There are some fainter glimmerings of hope. Perhaps some natural biological forces are at work which may reduce the need for full-scale human interference. In Lake Huron, for instance, the blood-suckers may be running low on food. They are getting smaller each year. Stranger still, their sex ratio has changed strikingly. From the approximately balanced ratio of males to females expected in nature the sea-lamprey runs have shown a marked trend toward male predominance. One well-documented total run of nearly twenty-five thousand animals had a sex ratio of 214 males to 100 females. We don't know the cause of this phenomenon but are interested because of the possibility that, if the trend continues at or near the present rate, it will adversely affect the beast's reproductive potential. We hope so, for the lowest estimate for total control on the United States side alone is a capital investment of a million and a half dollars plus five hundred thousand yearly for operation of devices, restoration of the fishery, and continued research.

Already the Federal Government of the United States has poured some $1,750,000 into sea lamprey research and control and experimental lake trout marking and planting. The individual states have been spending at the rate of about fifty thousand dollars a year and are preparing to participate in rehabilitation through fish hatching and stocking to the tune of about five hundred thousand dollars a year. On the other side of the lakes, the Canadian province of Ontario has for several years assigned a few men and about ten thousand dollars for trapping spawning migrants; in 1953 the Federal Government of Canada stepped in with more than three hundred thousand dollars to begin full-scale control.

With reconstruction of the Welland Canal in prospect, perhaps the engineers can devise some method of lamprey-proofing the original and artificial ingress from the sea.

Using the valuable lake trout as an example of the consequence of lamprey depredations may give an over-simplified idea of the whole situation. Though annual losses to fishermen from lake trout destruction total more than two and a half million dollars a year, damage to most of the other important commercial species has increased as the lake trout have declined. As in any biological complex where an imbalance is artificially induced, some startling changes have taken place. The lake trout is a carnivorous fish, and when abundant found ample food among the herring-like fish of the lakes, commonly called "chubs." Now, with nothing to keep them down, the chubs, too, have multiplied far beyond any market for these second-rate fish.

Those long-gone engineers at the opening of a canal and a burgeoning economic era opened a veritable Pandora's box. We hope we can slam the lid in time. ◆ ◆ ◆

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Preliminary Notes on the Culturing of *Gymnodinium brevis* Davis

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The mass mortality of fish off the west coast of southern Florida has attracted widespread attention since 1946. These catastrophes, commonly called Red Tides, have been associated with the high incidence of the marine dinoflagellate *Gymnodinium brevis* Davis (*1*) in the plankton populations (*2, 3*). Other investigators have reported conditions associated with these plankton blooms (*4–8*), but the study of this protist has been curtailed because of its sporadic occurrence in nature and the difficulty of maintaining it in laboratory culture.

Preliminary field investigations and culturing of a related species, *Gymnodinium splendens*, provided information that simplified the culturing of *G. brevis*. A medium composed of sea water, vitamin B_{12} (0.05 µg/100 ml), and Van Niel's (*9*) medium for sulfur bacteria (diluted 500 times) produced a culture containing more than 2500 cells of *G. splendens* per milliliter from an initial inoculum of two cells per milliliter in about 6 wk. *Gymnodinium brevis* responded better when the components of Van Niel's sulfur bacteria medium were diluted 1000 times and the vitamin B_{12} was increased to 0.1 µg/100 ml. The vitamin-B_{12} requirement of algal flagellates is discussed by Hutner and Provasoli (*10*). Vitamin B_{12} was required by dinoflagellates grown in pure culture by Provasoli *et al.* (*11*) and by Sweeney (*12*).

Using the latter medium as a base and a standard, we tested inorganic compounds, organic compounds, vitamins, and extracts of materials known to occur in nature, for example, soil and fish. By adding Florida peat extract, results were improved, but repeated experiments gave inconsistent results. A hot-water extract of beef liver further increased growth. We later substituted thiamine and biotin for the liver extract. The addition of the disodium salt of ethylenediamine tetraacetic acid (EDTA · Na), a metal buffer, (also designated ethylenedinitrilo tetraacetic acid disodium salt) increased the reliability of growth and resulted in the medium of Table 1. Soil extract, a more generally available material, can be substituted for Florida peat extract with a slight reduction in growth.

The conditions that we employed for culturing *G. brevis* are as follows: (i) Screw-cap test tubes 15 mm by 120 mm without liners were used for most experiments. Mass cultures are grown in erlenmeyer flasks and 5-gal Pyrex bottles with polyethylene covers (prepared by heating polyethylene sheet until soft and then molding over the mouth of the container). The glassware is cleaned by immersion in alcohol and sodium hydroxide solution, allowed to simmer 30 to 40 min in a solution of Cleaning Compound, No. 3298 (Arthur H. Thomas Co.), and rinsed 10 times with tap water and 15 times with distilled water. Extensive rinsing is employed since erratic results may be caused by minor contamination. (ii) Sterilization by steaming for 30 min on three successive days is optimum for the growth of *G. brevis*. McLaughlin (*13*) shortens the time by allowing 4-hr intervals between three 1-hr steaming periods without affecting growth results. Autoclaving produces erratic results. Growth is more consistent if inoculation is delayed for 4 days after sterilization. (iii) Aged sea water from the Gulf of Mexico [salinity, 36.5 parts per thousand (ppt)] was used in all experiments. The salinity of natural water containing high concentrations of *G. brevis* is usually between 32 and 34 ppt. A medium prepared according to Table 1 has a salinity of approximately 32 ppt. (iv) The temperature was usually maintained between 26° and 28°C, with as little variation as possible. (v) The *p*H stabilizes between 7.7 and 7.9 after sterilization. The *p*H of our aged sea water was between 8.1 and 8.2. The decreased *p*H is brought about by adding EDTA · Na. (vi) White daylight fluorescent tubes, 40-w, were used to maintain a light intensity of 175 to 300 ft-ca. (vii) Neither agitation nor aeration is required for growth. (viii) *G. brevis* was isolated into a unialgal culture in September 1953 and has been continuously subcultured since that time. Cultures usually reach maximum growth in 6 wk.

By substituting a group of trace metals (Fe, Zn, Mn, Sr, Rb, Mo, Co, Cu, Cr, Ti, Al, Si, and Zr) for soil extract, we obtained a medium that supports good initial growth of *G. brevis*, but continuous subculturing has not been successful. Titanium and zirconium were added to the mixture, although they are not normally present in measurable amounts in sea water (*14*), because these metals were found abundantly in water of *G. brevis* blooms (*7*).

Investigations led us to believe that heavy rainfall and subsequent river discharge are instrumental in

Table 1. Medium for the unialgal isolation of *G. brevis* Davis. After all additions are made, there is approximately 110 ml of medium.

Aged sea water (salinity, about 36.5 ppt)	95.0 ml
Distilled water*	5.0 ml
NH_4Cl†	0.1 mg
KH_2PO_4†	0.05 mg
$MgCl_2 \cdot 6H_2O$†	0.02 mg
$NaHCO_3$†	0.1 mg
$Na_2S \cdot 9H_2O$†	0.1 mg
Vitamin B_{12}	0.1 µg
Thiamine hydrochloride	1.0 mg
Biotin	0.05 µg
Soil extract‡	2.0 ml
EDTA · Na (6 ml of 0.25-percent solution)	15.0 mg

* More or less may be required, depending on the salinity.

† Added as 0.5 ml of the following solution of the components of Van Niel's medium for sulfur bacteria: NH_4Cl, 0.2 g; KH_2PO_4, 0.1 g; $MgCl_2 \cdot 6H_2O$, 0.04 g; $NaHCO_3$, 0.1 g; and $Na_2S \cdot 9H_2O$, 0.2 g to 1 lit of distilled water.

‡ Simmer for 40 min a mixture of 500 g of garden soil and 1 lit of distilled water. Let it stand for 4 days and decant the supernatant. Repeat simmering and decantation until extract is clear. Our soil gives a yellowish-brown extract.

initiating a bloom of *G. brevis* (*8, 15, 16*). On the basis of this belief, we conducted culture experiments whereby mediums were prepared by adding river water, extracts of peat soils from the western Florida coastal region, or both, to sea water from the Gulf of Mexico. Sea water containing 4 to 10 ml of river water per 100 ml supported limited growth of *G. brevis*. Seven to 10 ml of river water or peat extract per 100 ml of sea water is better, and peat extract or mixtures of peat extract and river water at this concentration are more productive than river water alone. The addition of vitamin B_{12} (0.05 μg/100 ml of medium) improved the reproducibility and growth.

The conditions in a bloom of *G. brevis* often led us to believe that fish which had been killed and subsequently decayed imparted nutrients that helped to perpetuate the bloom. We designed culture experiments to determine whether extracts of partially decayed fish promoted growth. The results of these experiments indicate that the extracts contain one or more growth-promoting substances. Robinson (*17*) lists fish, or portions thereof, as containing vitamins B_{12}, biotin, thiamine, and other B-complex vitamins.

Laboratory cultures of *G. brevis* have attained homogeneous concentrations exceeding 2 million cells per liter. This concentration is far below the highest report (*2, 3*); however, the values cannot be compared. Among other reasons, *G. brevis* in cultures concentrate to form masses that we disperse by shaking before making counts. A similar tendency to concentrate, but on a larger scale, may be expected in nature. Counts of a sample from such a concentration would be high. Ketchum (*5*) considered a tendency of the organism to concentrate as a possible cause of high surface organic phosphorus concentrations.

Mass cultures of *G. brevis* maintained in this laboratory are toxic to fish. We conducted toxicity experiments using *Mollienesia sp.* and *Mambras vagrans* as test fish. Controls consisted of water taken at the collecting point of the fish and unialgal cultures of *G. splendens* containing more than 2.5 million cells per liter. All fish died in the water containing *G. brevis*, but none died in either of the controls. This experiment was repeated with the same results (*18*).

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Infectious Pancreatic Necrosis in Brook Trout

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During the winter and spring of 1954 several outbreaks of mortality were observed among fingerling brook trout in the eastern United States. These occurred soon after feeding of the fry started. The symptoms were characteristic for "acute catarrhal enteritis." * Some of the symptoms also resembled octomitiasis, but losses continued even after treatment for Octomitus was successful. Observations described in this article indicate that on the basis of histopathological examination the disease should be classified as an infectious pancreatic necrosis.

Pancreatic necrosis in mammals is generally credited to the action of pancreatic enzymes which are liberated from the ducts. The aberrant distribution of the enzymes has been attributed to a number of conditions including any anatomical arrangement which allows infected bile to flow into the main pancreatic duct.[3] Obstructions of small ducts within the pancreas may also lead to the condition,[4] or the initiating factor may be a mild bacterial infection or a focus of infarction in the pancreas due to thrombosis of diseased vessels.[5] Pappenheimer and coworkers [6] were the first workers to describe a specific pathogen for pancreatic necrosis. They reported that Coxsackie virus (Connecticut-5 strain) produced a highly selective pancreatic disease in adult mice. The present paper is a note on an additional infectious agent which produces specific pancreatic necrosis in brook trout.

MATERIALS AND EXPERIMENTS

In January, 1954, a disease occurred in the fingerling brook trout population at the Fish and Wildlife Service Station, Leetown, W. Va. The most characteristic symptom of the disease was a very violent whirling and corkscrewing motion, which suggested that the affected fish were literally writhing with pain. Mortality of infected lots in some cases reached 75%.

Grossly, the fish appeared normal with the exception of petechiae in the vicinity of the pyloric caeca. Routine examinations for bacteria and parasites were negative. Histologically, however, extreme pancreatic necrosis was observed.

The infected fish were in two groups from unrelated parent stock. In the first group, from Bellefonte, Pa., the epizootic started earlier, reached a peak in 10 to 12 days, then subsided over the continuing six-week period (Fig. 6). In the second group, from Berlin, N. H., the mortality started two weeks later, reached a peak in 10 to 12 days, and subsided somewhat more rapidly.

To test for transmission of the disease by water, fingerling brook trout were obtained from a third source of unrelated parent stock at Beaver Creek, Md. A trough was partitioned into two sections. The infected Berlin group was placed in the upper section of the trough and 565 of the Beaver Creek group were placed in the lower section. Typical symptoms of the disease developed in the exposed group 6 days later, and the mortality reached a peak in 10 to 14 days. Acute pancreatic necrosis was observed in both groups histologically.

In July, the disease occurred in two West Virginia hatcheries at Dorcas and Marlington. The infected fish showed typical symptoms of the disease; the mortality curve reached a peak in 10 to 14 days, and acute pancreatic necrosis was observed histologically. At the time of writing this paper (January, 1955) reports indicate that the disease may be even more widely spread this year.

PATHOLOGY

Gross Lesions.—An unusual feature of this disease is the extremely high mortality

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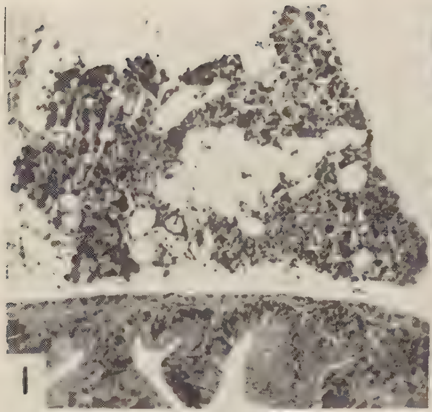
Salmon Nutrition Laboratory, Cook, Wash., and Microbiological Laboratory, Leetown (P. O. Kearneysville) W. Va.

* References 1 and 2.



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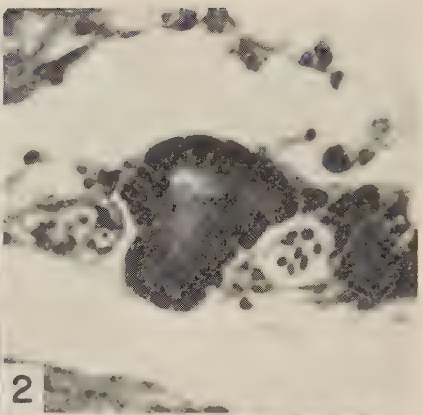

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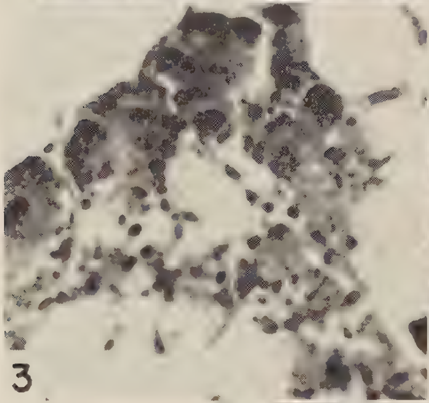

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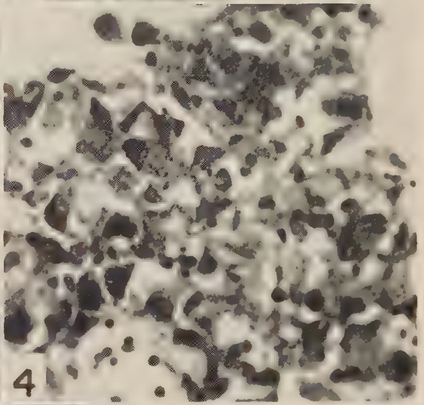

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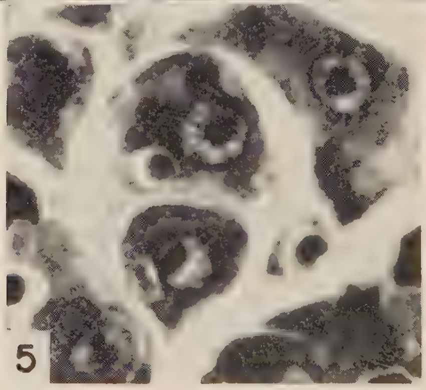

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Fig. 1.—Necrotic pancreatic tissue adjacent to a pyloric caeca. Hematoxylin and eosin; × 100.

Fig. 2.—An unaffected foci of acinar cells. Hematoxylin and eosin; × 400.

Fig. 3.—A relatively early stage of the disease showing the edge of the advancing necrosis. Hematoxylin and eosin; × 400.

Fig. 4.—An advanced stage of the necrosis. Hematoxylin and eosin; × 400.

Fig. 5.—Inclusion bodies in acinar cells at the edge of the advancing necrosis. Hematoxylin and eosin; × 1350.

which occurs with practically no grossly observable lesions. Small petechiae in the vicinity of the pyloric caeca are the only visible abnormalities. In fish, the pancreas is not a distinct, encapsulated organ. The acinar tissue and islets are scattered throughout the mass of pyloric caeca, which are grouped about the small intestine immediately below the juncture with the stomach. The minute hemorrhages occur in this tissue.

Microscopic Lesions.—The microscopic picture is practically identical to that described by Pappenheimer and co-workers[6] for pancreatic necrosis in mice injected with Coxsackie virus. In many fish the major portion of the acinar tissue is obliterated by a massive necrosis. The entire acinar structure is replaced by a mass of necrotic detritus containing fragmented acinar cells, pyknotic nuclei, and zymogen granules (Figs. 1 to 4). The cytoplasm and detritus are markedly eosinophilic. In advanced cases there is a marked cellular reaction consisting primarily of monocytes but with a few polymorphonuclears present. Fat deposits, which are commonly found infiltrating and surrounding the pancreatic tissue of hatchery fish, show an extensive fat necrosis, presumably from the lipolytic enzymes. In contrast to Pappenheimer's observations, however, the islet tissue is not entirely spared. Not infrequently, extensive necrosis also occurs within the islets. Small ducts within the necrotic areas usually appear unharmed.

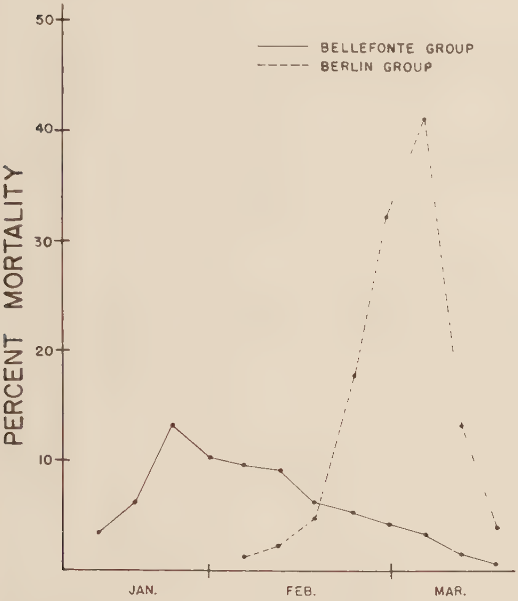

Fig. 6.—Per cent mortalities calculated for five-day periods.

The initial stage of the necrosis does not start from a single focus of infection. Instead, small foci are scattered widely throughout the acinar structure. These rapidly encroach on the surrounding tissue. At the periphery of these areas of necrosis many acinar cells contain intercytoplasmic inclusions. These are small, blue, usually oval bodies surrounded by a clear halo (Fig. 5). The definite location of these inclusions at the edge of the advancing necrosis may indicate a relationship to the causative agent.

No other organs show any significant changes, grossly or histologically.

COMMENT AND SUMMARY

An infectious disease highly specific for the pancreas of young brook trout has been observed. The lesions are those of massive necrosis of the acinar and islet tissues. The complete absence of bacteria or parasites in infected fish suggests that a virus may be the causative agent. The similarity of the lesions to those described by Pappenheimer and coworkers[6] following the injection of Coxsackie virus in adult mice also lends credence to this possibility. Neither is it inferred at the present time nor is the possibility overlooked that the inclusion bodies observed in acinar cells at the periphery of necrotic areas are true virus inclusion bodies. Further studies are in progress to clarify the etiologic agent.

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SULFONAMIDE TOXICITY IN BROOK TROUT

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Abstract

Sterility was observed in female brook trout that were treated with sulfamerazine at frequent intervals for 2 years to control endemic furunculosis. Feeding sulfamerazine for a period of 8 months caused massive kidney damage similar to that observed in humans who develop allergies to "sulfa" drugs. Kidney damage of the type observed would probably cause renal insufficiency which would handicap any physiological function including reproduction. Feeding sulfonamides for periods up to 13 weeks did not produce kidney damage.

Introduction

Sulfonamide toxicity has been recognized and documented frequently in the therapy of humans and domestic animals With the increasing use of these drugs for the control of fish diseases various workers have cautioned that indiscriminate feeding would be harmful. Gutsell and Snieszko (1949) noted a decreased growth rate on diets containing sulfamerazine. This effect was most apparent with brown trout (*Salmo trutta*). Snieszko (1952) observed that the long-range prophylactic use of antibiotics might result in drug-resistant strains of pathogens and would also be toxic to the treated fish. Heavy mortality of coho salmon fingerlings (*Oncorhynchus kisutch*) after treatment with sulfamerazine was reported by Johnson and Brice (1953). The effect on growth of three species of trout by several sulfonamides has been described by Snieszko and Wood (1955).

Among the most common undesirable reactions in humans are those due to hypersensitivity and allergy which may be manifested in many different forms, all rather non-specific and difficult to diagnose. Kidney damage may result from allergic reactions or from the mechanical obstruction of precipitated sulfonamide crystals which may lead to symptoms of renal insufficiency. In fish, poor growth due to sulfonamides has

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generally been attributed to reduced consumption of food and the causes of mortality have not been determined.

An unusual case which very likely resulted from sulfa toxicity was reported by a Maryland State Fish Hatchery in January 1953. To control endemic furunculosis in young brood stock of brook trout (*Salvelinus fontinalis*), sulfamerazine had been fed prophylactically for several days every month for 2 years. As the first spawning season approached the fish appeared to be maturing normally. The females became enlarged and felt "ripe" to experienced spawntakers. No eggs were obtained, however, and when it became evident that the eggs were being resorbed, the fish were taken to the Fish and Wildlife Service Experimental Station at Leetown, West Virginia, for examination.

A gross examination revealed no abnormal pathology. The ovaries and testes were in a normal stage of retrogression. Eggs were being resorbed in all females examined as would be expected in mid-January if spawning had not occurred the previous fall. The advanced stage of this process made it impossible to determine whether the eggs had reached full maturation before resorption began. All other organs were apparently normal. Histological examination, however, revealed massive kidney damage somewhat similar to the lesions observed in mammals after excessive "sulfa" therapy. These observations prompted an experimental program to determine under what conditions tissue damage could be caused in trout by over-medication with sulfa drugs.

METHODS

Experiment 1.—On June 24, 1953, sulfamerazine treatments were started on two lots of fingerling brook trout. In both lots the fish were fed 8 grams of sulfamerazine per 100 pounds of trout per day (about 175 milligrams per kilogram trout). Lot No. 1 was fed the drug on Mondays and Tuesdays of each week. Lot No. 2 was treated for 1 full week (the first week) each month. Each group was given approximately the same total amount of sulfamerazine during the experiment. The only variable between the two lots was the frequency of medication. Samples were removed for histological examination after 16, 26, and 34 weeks of medication. The total course of the experiment was approximately 8 months.

Experiment 2.—On April 12, 1954, duplicate lots of fingerling brook trout, brown trout, and rainbow trout (*Salmo gairdneri*) were started on diets containing the following drugs: sulfamerazine, sulfisoxazole (Gantrisin), sulfamerazine (6 parts) and sulfaguanidine (4 parts). All sulfonamides were given at a rate of 9 grams per 100 pounds of trout per day (200 milligrams per kilogram of trout). Duplicate controls were fed the same diets without sulfa drugs. The brook trout and rainbow trout were maintained on this experiment for 8 weeks; the brown trout were continued for an additional 5 weeks. This experiment was designed to test the effect of sulfonamides over a relatively short period of time. The dosage was only slightly higher, but the amount of drug given per month was about five times greater than that used in Experiment 1.

Tissues were fixed in Bouin's solution for 24 hours and stored in 65-percent alcohol. Paraffin sections were stained with hematoxylin and eosin, and by the Dunn-Thompson and Okajima methods for hemoglobin (Lillie, 1948). Sulfonamide-specific stains were not used due to difficulties of proper fixation and a lack of freeze-drying equipment.

Effects of Sulfonamides

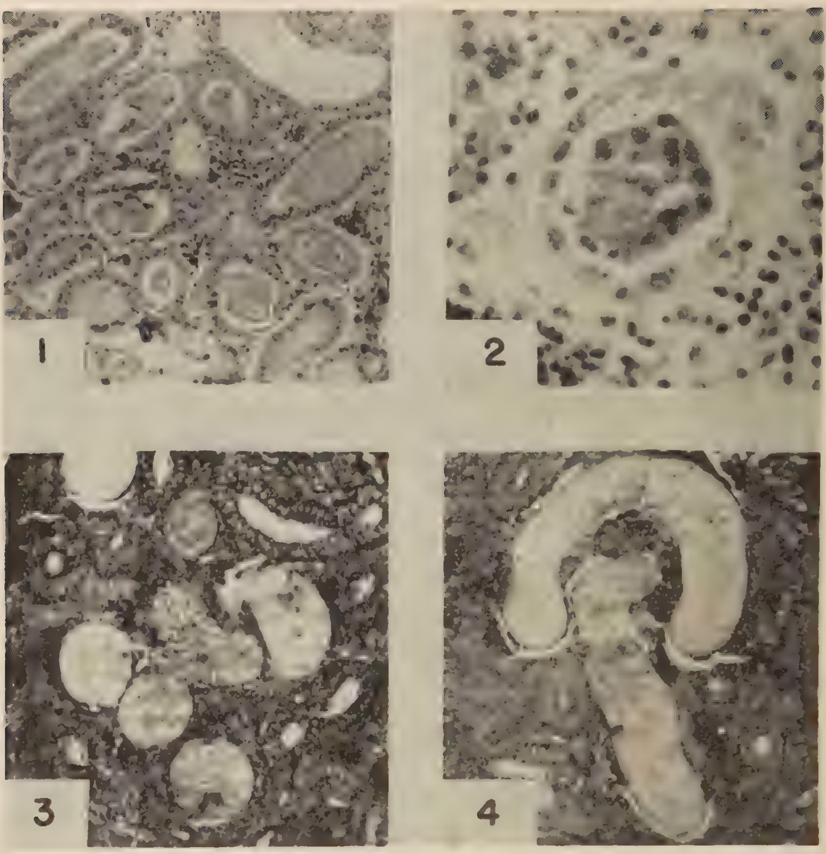
A striking feature of the kidney lesions observed in the Maryland trout, which had been fed sulfamerazine prophylactically for 2 years, was an extensive tubular degeneration (Figs. 3 and 4). In hematoxylin and eosin sections these tubules appeared as opaque, necrotic, white or light-yellow structures with all cellular detail obscured. The degeneration began in the proximal parts of the convoluted tubules and extended to the distal portions where it appeared to be in a more advanced stage. Combined with these lesions were large numbers of small globular masses scattered throughout the hematopoietic tissue (Figs. 7 and 8). These masses stained bright red with eosin and were acellular. When hemoglobin-specific stains were used, both the globular masses and degenerate tubules stained hemoglobin-positive. The globular masses appeared to be entirely hemoglobin, whereas the degenerate tubules seemed to be completely impregnated with the blood pigment. In less advanced cases, entire erythrocytes were occasionally seen in the tubule lumens. No sulfonamide crystals were observed.

Experiment 1.—The sample taken after approximately 16 weeks of sulfa medication did not show pathology related to the experimental therapy. After 26 and 34 weeks, the brook trout exhibited pathology similar to that observed in the Maryland fish, although the lesions appeared to be earlier forms or less severe. Well defined casts and degeneration of tubular epithelium were observed in both samples (Figs. 1 and 2). However, discrete masses of hemoglobin were observed in the hematopoietic tissue in the last collection only (Figs. 5 and 6). Tubules permeated with hemoglobin were not observed in any of the experimental fish. Sulfonamide crystals were not observed. The incidence of kidney lesions was slightly greater in the group fed sulfamerazine twice daily.

Experiment 2.—No pathological condition was observed in any experimental group that could be correlated with sulfonamide toxicity.

Danger of Continued High-Level Treatment

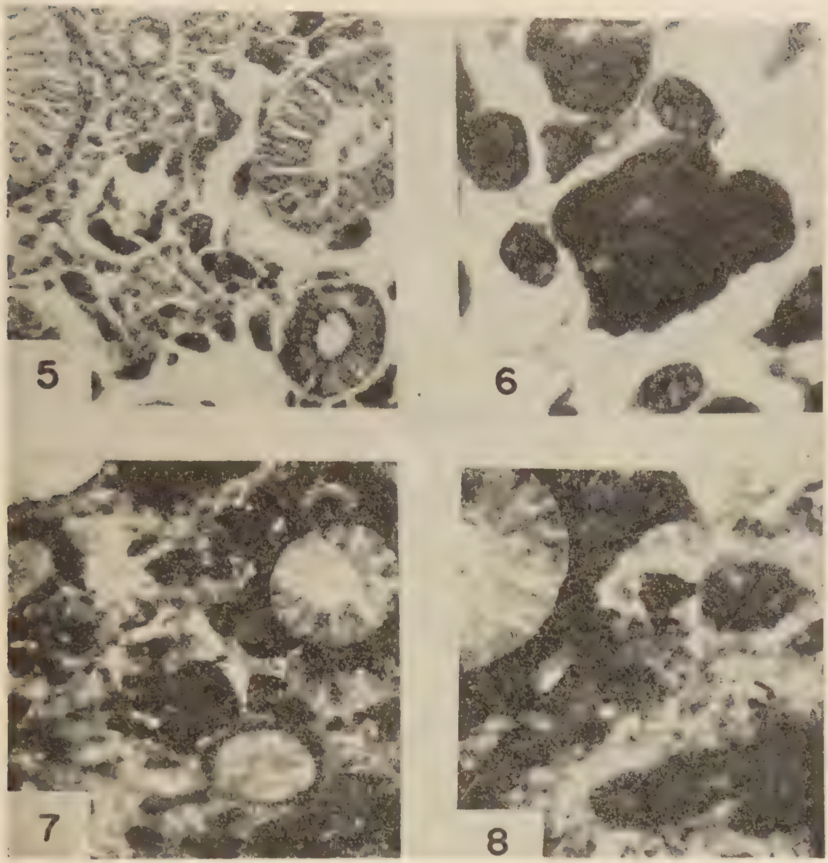
The kidney lesions in humans and domestic mammals caused by sulfonamide toxicity bear some resemblance to those observed in fish that have been fed excessive amounts of sulfa drugs. The renal reaction to the sulfonamides that is of most concern to humans, both because of its frequency and its gravity, is hemoglobinuric nephrosis (Allen, 1951). This condition is characterized by casts of hemoglobin or related pigment



FIGURES 1–4.—Kidney lesions in brook trout. 1. Casts in tubules and tubule degeneration after 26 weeks of sulfamerazine medication. Experiment 1. Hematoxylin and eosin x 100. 2. Degenerating erythrocytes in tubule. Experiment 1. Hematoxylin and eosin x 400. 3 and 4. Tubules permeated with hemoglobin after 2 years of medication. Maryland fish. Okajima stain x 200.

globins in the distal convoluted or collecting tubules. The massive deposits of hemoglobin seen in both the hematopoietic and renal tissues of fish are not morphologically similar to the casts of hemoglobinuric nephroses; thus the etiology of the lesion is possibly not the same as that observed in mammals. It appears likely, however, that the lesions in fish are associated with allergic reactions, as are similar lesions in mammals. The absence of sulfonamide crystals may be due to the histologic processing since the crystals are water-soluble.

Tissue damage in fish is apparently caused by sulfonamides, but only after remarkably long periods of medication at relatively high dosages.



FIGURES 5–8.—Kidney lesions in brook trout. 5. Hemoglobin in hematopoietic tissue of kidney after 34 weeks of medication. Experiment 1. Okajima stain x 200. 6. Same as Fig. 5 x 400. 7. Hemoglobin in hematopoietic tissue after 2 years of medication. Maryland fish. Okajima stain x 200. 8. Same as Fig. 7 x 400.

The feeding level of sulfamerazine in Experiment 2 was approximately twice the normal dosage prescribed for humans, but apparently the period of medication was too short to develop kidney lesions. The tolerance to such high levels might be explained by poor intestinal absorption, but Snieszko and Friddle (1951) have shown that high tissue levels do result. They observed blood concentrations as high as 25.0 milligrams percent following 9 days of medication at the rate of 200 milligrams of sulfamerazine per kilogram of trout. In human patients, blood levels of 10 to 15 milligrams percent are induced only when the danger from disease outweighs the increased danger of toxic effects.

Despite the relatively high resistance of trout to sulfonamide toxicity, it has been demonstrated that prolonged usage will damage the kidney. The evidence from the Maryland fish that over-medication will cause sterility has not been confirmed experimentally. However, kidney damage of the degree observed in the Maryland fish would undoubtedly result in renal insufficiency severe enough to place a systemic handicap on any physiological function. That normal reproduction would be affected adversely as a secondary effect is entirely possible.

It appears that the continued use of sulfa drugs at low levels over long periods is more harmful than high levels for short periods. The results obtained experimentally by feeding sulfamerazine at two frequencies for long periods were not sufficiently different to permit a recommendation based on either frequency. Both methods of feeding led to kidney damage.

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